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Comparison of three recurrent selection regimes for increasing groat-oil content of oat

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TABLE OF CONTENTS

GENERAL INTRODUCTION

Recurrent selection is a breeding method designed to change the mean of a quantitatively inherited trait in a population of plants by increasing the frequency of favorable alleles (Hallauer, 1985). The procedure is cyclical and repetitive. A cycle involves three steps: (1) developing progenies, (2) testing progenies, and (3) recombining selected progenies. Step 3 ensures the continuous presence of genetic variability in the population. A variety of recurrent selection procedures has been used for both allogamous and autogamous crops. The choice of procedure depends on the heritability and type of gene action of the trait under selection and the type of cultivar utilized.

Eberhart (1970) derived a formula to predict annual genetic gains from different recurrent selection procedures:

$$\Delta G = (i\ c\ \sigma_A^2) \ /\ (\sigma_P\ y)$$

In this formula, i is the standardized selection differential, c is the parental control factor, σ_A^2 is the additive genetic variance among the progenies, σ_P is the phenotypic standard deviation among the progenies, and y is the number of years needed to complete a cycle of recurrent selection. The parameters in the formula can be manipulated to maximize genetic gain. Parameters i and c are determined, respectively, by the fraction of the population that is selected and by the type of progenies recombined. The σ_A^2

depends on the type of progenies tested (individual plants, HS or FS families, inbred progenies), and the σ_p on the precision of the evaluation experiment. The time required to complete a cycle of selection conditions y. To reduce cycle time in recurrent selection programs for highly heritable traits, greenhouses can be utilized for evaluation (Byrne and Rasmusson, 1974; Crosbie et al., 1981; Burton and Brim, 1981; Avey et al., 1982).

Oil content of groats (caryopses) of oat (Avena sativa L.) is a quantitatively inherited trait (Frey et al., 1975) with primarily additive gene action (Elliot et al., 1985; Thro and Frey, 1985), and it is highly heritable (Baker and McKenzie, 1972; Brown et al., 1974; Branson and Frey, 1989a). Further, Youngs and Forsberg (1979), Thro and Frey (1985), and Gullord (1986) reported low genotype-environment interaction for groat-oil content over a range of environments. Groat-oil content in oat, therefore, should be suitable for evaluation in a greenhouse.

Because of its high quality protein and oil, oat is regarded as highly nutritious compared with other cereals (Weber, 1973; Price and Parson, 1975; Peterson, 1976). Oat oil has a low proportion of linolenate and a high proportion of oleate and linoleate, and it is, therefore, a good culinary oil (Kalbasi-Ashtari and Hammond, 1977). Groat-oil contents in oat cultivars currently grown in Midwestern U.S.A., range from 40 to 60 g kg^{-1} which is too low for

economic extraction. Brown et al. (1966), however, showed that groat-oil contents varied from 39 to 90 g kg^{-1} in 169 oat strains grown in Illinois, but Frey and Hammond (1975) estimated that groat-oil contents as high as 160 g kg^{-1} are necessary to make oil extraction profitable. In an oat population with sufficient genetic variability for groat-oil content, recurrent selection is probably the best alternative method to obtain oat lines with groat-oil contents high enough to make oat an oilseed crop. In soybean [Glycine max (L.) Merr.], maize (Zea mays L.), and oat, recurrent selection for oil content has been effective (Burton and Brim, 1981; Misevic and Alexander, 1989; Branson and Frey, 1989a).

The research presented in this dissertation evaluates the efficacy of three recurrent selection regimes for increasing groat-oil content in oat. The respective regimes are:

1. Selection among S_0 plants evaluated in the field and intermating selected $S_{0:1}$ lines in the greenhouse;
2. Same as in (1) except that selection is among S_0 plants evaluated in the greenhouse; and
3. Selection among S_0 plants grown in the field followed by selection among and within selected $S_{0:1}$ progenies evaluated in the greenhouse, and intermating selected $S_{1:2}$ lines also in the greenhouse.

The specific objectives were to:

1. Estimate the genetic correlation between groat-oil contents of field- and greenhouse-grown oat plants;
2. Predict the genetic gains in groat-oil content from the three recurrent selection regimes;
3. Evaluate the actual gains in groat-oil content from the three recurrent selection regimes;
4. Determine degrees of correlated changes in unselected agronomic traits when the three recurrent selection regimes are used;
5. Identify changes in the fatty acid composition associated with selection for groat-oil content in recurrent selection regime 1; and
6. Develop oat strains that are high in groat-oil content and that can be grown as an oilseed crop.

REVIEW OF LITERATURE

Oat (Avena sativa L.) is grown primarily in the temperate zone of the Northern Hemisphere. In 1980, 526000 ha of oat were planted in Iowa (Youngs and Forsberg, 1987). About 85% of the oat crop harvested for grain is used for livestock feed, and about 10% for human consumption (Forsberg and Shands, 1989). Compared with other cereals oat is highly nutritious because of its high quality protein (Peterson, 1976) and high oil content (Weber, 1973; Price and Parson, 1975). Frey and Hammond (1975) suggested that oat might be grown as a profitable oilseed crop in Iowa if the groat (caryopsis) oil content was 160 g kg^{-1}. Groat-oil contents in currently grown oat cultivars, however, range from 40 to 60 g kg^{-1}. Therefore, an efficient breeding procedure must be employed to obtain an oat that has 160 g kg^{-1} groat-oil.

Oil in Groats of Oat

There is a considerable range in groat-oil contents of oat. Brown et al. (1966) found that oil contents in primary groats of 169 oat strains grown in Illinois varied from 39 to 90 g kg^{-1}. Kernel-oil contents in Corn Belt maize (Zea mays L.) hybrids range from 40 to 50 g kg^{-1} (Alexander, 1988) whereas the seed-oil content in soybean [Glycine max (L.) Merr.] generally is about 200 g kg^{-1} (Fehr, 1987). Oil content in other small grains such as wheat (Triticum

aestivum L.), barley (Hordeum vulgare L.), rice (Oryza sativa L), and rye (Secale cereale L.) is about 20 g kg^{-1} (Hutchinson and Martin, 1955).

The oat groat can be separated into four parts: embryonic axis, scutellum, bran, and endosperm. The first two parts are collectively the germ fraction which constitutes about 4% of the groat (Youngs, 1972). Youngs et al. (1977) studied two Wisconsin oat cultivars, and found that the germ fraction contained the highest concentration of oil but because the bran and endosperm make up 96% of the oat groat, they contained more than 90% of the oil.

Triacylglycerols make up the predominant portion of groat-oil in oat (Youngs and Forsberg, 1987). Triacylglycerol is a glycerol molecule that has different or identical fatty acids esterified to the three OH-positions. The quality of oil is determined by its relative contents of different fatty acids (Appelqvist, 1989). Youngs and Püskülcü (1976) found a considerable variation in the fatty acid composition of groat-oil from 15 oat strains grown in the U.S.A.. The ranges were 4 to 8 g kg^{-1} for myristate (14:0), 162 to 218 g kg^{-1} for palmitate (16:0), 12 to 20 g kg^{-1} for stearate (18:0), 284 to 403 g kg^{-1} for oleate (18:1), 366 to 458 g kg^{-1} for linoleate (18:2), and 15 to 25 g kg^{-1} for linolenate (18:3). (The first number in the shorthand designation of the fatty acids indicates the number of carbons and the second the number of double bonds. Fatty

acids with double bonds are called unsaturated.)

In most vegetable oils, stearate is synthesized by elongation of palmitate, and it is the precursor of oleate which, in turn, is the precursor of linoleate and linolenate (Lehninger, 1982). Polyunsaturated fatty acids are essential in mammalian diets because mammals cannot convert oleate into linoleate and linolenate (Lehninger, 1982). Linoleate reduces plasma cholesterol levels (Hegsted et al., 1965) and cures dermatitis in humans (Guthrie, 1989). Linoleate and linolenate both promote growth (Guthrie, 1989). A high proportion of linolenate in an oil is undesirable, however, because it oxidizes easily resulting in rancidity of the oil (deMan, 1990). Monounsaturated fatty acids, and specifically oleate, have been shown to prevent coronary heart disease (Grundy, 1987). Saturated fatty acids increase the risk for coronary heart disease because they elevate the plasma cholesterol level. However, Bonanome and Grundy (1988) demonstrated that stearate effectively reduces the plasma cholesterol level. It is recommended that human diets should have about equal proportions of saturated, monounsaturated, and polyunsaturated fatty acids (Vles and Gottenbos, 1989).

Fatty acid profiles of canola (Brassica spp.), sunflower (Helianthus annuus L.), safflower (Carthamus tinctorius L.), soybean, olive (Olea europaea L.), peanut (Arachis hypogaea L.), maize, cottonseed (Gossypium spp.), palm (Acrocomia aculeata Jacq.), and oat are presented in Table 1. Canola

Table 1. Fatty acid profiles (in g kg^{-1}) of common vegetable oils[a] and oat oil[b]

Crop	Fatty acids													
	Saturated						Monounsaturated					Poly-unsaturated		
	14:0	16:0	18:0	20:0	22:0	Tot.	16:1	18:1	20:1	22:1	Tot.	18:2	18:3	Tot.
Canola	-	40	20	-	-	60	-	550	20	10	580	260	100	360
Sunflower	-	40	30	-	-	70	-	340	-	-	340	590	-	590
Safflower	-	80	30	-	-	110	-	130	-	-	130	750	10	760
Soybean	-	110	40	-	-	150	-	250	-	-	250	510	90	600
Olive	-	140	20	-	-	160	20	660	-	-	680	160	-	160
Peanut	-	60	50	20	30	170	-	610	-	-	610	220	-	220
Maize	-	130	40	-	-	170	-	290	-	-	290	540	-	540
Cottonseed	10	290	40	-	-	340	20	240	-	-	260	400	-	400
Palm	10	480	40	-	-	530	-	380	-	-	380	90	-	90
Oat	10	190	20	-	-	220	-	360	-	-	360	400	20	420

[a]Adapted from deMan (1990)

[b]Adapted from Youngs and Püskülcü (1976)

and soybean oils contain high levels of linolenate which makes them unstable (deMan, 1990). Palm oil is high in saturated fatty acids whereas olive, peanut, and canola oil are high in monounsaturated fatty acids. Safflower, sunflower, soybean, and maize oil are high in polyunsaturated fatty acids. Cottonseed and oat have the most balanced oils with respect to saturated, monounsaturated, and polyunsaturated fatty acids.

Beside triacylglycerols, oat oil contains small amounts of diacyl- and monoacylglycerols and phospho- and glycolipids (Youngs and Forsberg, 1987). The latter substances are often rich in polyunsaturated fatty acids (Appelqvist, 1989) and cause processing problems (Hammond, 1983). Lipase is an enzyme that splits fatty acids from the glycerol molecule. This results in high levels of free fatty acids which causes rancidity of the oil (Hutchinson and Martin, 1952). Frey and Hammond (1975) screened 352 oat strains and found considerable variation for lipase activity. They concluded that breeding for low or high levels of lipase should be possible.

Genetics of Groat-oil Content

The inheritance of groat-oil content in oat has been investigated extensively. In a diallel of eight A. sativa parents, Brown et al. (1974) found that groat-oil content was under polygenic control and that gene action was largely

additive. Elliot et al. (1985) conducted a diallel with four A. sativa and two A. sterilis parents and concluded that the major source of variation was for general combining ability. Frey et al. (1975) using three interspecific matings of A. sativa with A. sterilis, detected polygenic inheritance and partial dominance for groat-oil content. Frey and Hammond (1975) arrived at a similar conclusion, but Thro and Frey (1985) found no evidence for dominance nor epistasis in a generation mean analysis of three A. sativa matings.

Based on limited data, Brown and Aryeetey (1973) concluded that groat-oil content was largely determined by the maternal genotype and that cytoplasmic effects were not important. Brown et al. (1974) did not find cytoplasmatic effects either.

Groat-oil content is determined largely by genetic effects. Heritability for groat-oil content generally is high (Stuke, 1961; Baker and McKenzie, 1972; Brown et al., 1974). In an A. sativa population with A. sterilis alleles for oil content introgressed in it, Branson and Frey (1989a) found a realized heritability of 0.68 after three cycles of phenotypic recurrent selection. Further, several investigators (Stuke, 1961; Baker and McKenzie, 1972; Frey and Hammond, 1975; Youngs and Forsberg, 1979; Thro and Frey, 1984; Gullord, 1986) found that genotype-environment interaction for groat-oil content was consistently low over a range of studies.

The consensus is that groat-oil content is (1) polygenically controlled, (2) determined mainly by additive gene action, (3) highly heritable, and (4) stable over environments. This indicates that recurrent selection based upon evaluations of S_0 plants grown in a single environment should be effective.

Correlations of Groat-oil Content with Agronomic Traits

Penning de Vries et al. (1974) concluded that 1 g of glucose is required to produce either 0.826 g carbohydrate, 0.404 g protein, or 0.330 g oil. Applying this result, Bhatia and Rabson (1976) computed production values, or ratios of weight of end-product to weight of required substrate. Based on calculations of production values, Mitra and Bhatia (1979) found that the bioenergetic cost of increasing the oil content in seed was maximal when the increase was at the expense of carbohydrate content and minimal when oil content increased at the expense of protein content. If the rate of photosynthate production is constant, oat plants with a higher groat-oil content should have a lower groat-protein content and/or a reduced grain yield. Therefore groat-oil content is expected to be negatively associated with groat-protein content and grain yield.

Significant negative correlations between oil and protein contents in groats of oat have been reported by Brown

et al. (1966) and by Rezai and Frey (1988) who studied 457 A. sterilis accessions. Forsberg et al. (1974), Welch (1974), Gullord (1980, 1986), and Elliot et al. (1985) reported mostly nonsignificant correlations. Youngs and Forsberg (1979) found no consistent relations between groat-oil and groat-protein contents. Forsberg et al. (1974), Gullord (1980), and Thro and Frey (1984) detected significant positive correlations between groat-oil content and grain yield, whereas Brown et al. (1966), Gullord (1986), and Branson and Frey (1989b) found mostly nonsignificant correlations.

Test weight of oat is the weight of a standard volume of seed and is used as a quality index. Negative associations between groat-oil content and test weight are therefore undesirable. Independence has been reported for these two traits by Brown et al. (1966), Forsberg et al. (1974), and Gullord (1980), whereas Branson and Frey (1989b) reported both independence and negative correlations.

Another important characteristic of oat is seed weight. Brown et al. (1966), Baker and McKenzie (1972), Forsberg et al. (1974), Welch (1974), and Gullord (1980) all reported nonsignificant associations between seed weight and groat-oil content. Branson and Frey (1989b), however, reported negative correlations.

In Iowa, oat cultivars with short stature and early maturity are favored. Groat-oil content was not correlated

with heading date or plant height in studies reported by Brown et al. (1966), Forsberg et al. (1974), Frey et al. (1975), Thro and Frey (1984), and Branson and Frey (1989b). Elliot et al. (1985) found that groat-oil content was positively correlated with heading date and plant height. A positive correlation with heading date also was found by Forsberg et al. (1974).

The correlations reported by Branson and Frey (1989b) are the only ones that came from a population under selection for groat-oil content. Long-term selection for a trait causes changes in the associations among selected and unselected traits (Falconer, 1981): Therefore, in a recurrent selection program associations among traits should be closely monitored.

Correlations of Groat-oil Content with Fatty Acids

Knowledge of correlations between groat-oil content and fatty acids is important because they indicate how various fatty acids might respond to increases in groat-oil content in oat. Forsberg et al. (1974) reported that in 10 oat lines groat-oil content was positively associated with oleate, negatively with palmitate, and was independent of stearate, linoleate, and linolenate. Welch (1975) found that the total fatty acid content in groats from greenhouse-grown plants was positively associated with the saturated and negatively with unsaturated fatty acids. Frey and Hammond (1975)

investigated 64 oat lines and found that groat-oil content correlated negatively with linoleate and linolenate, positively with oleate, but was not correlated with saturated fatty acids. Youngs and Püskülcü (1976) and de la Roche et al. (1977) found that groat-oil content was negatively correlated with palmitate and linoleate and positively with oleate. Groat-oil content was negatively related with linoleate and linolenate and positively with oleate in a study done by Karow and Forsberg (1984). Finally, Yarosh and Nizova (1988) showed that oil content was positively associated with oleate.

Based on the information from these six studies, selection for higher groat-oil content might result in decreases in palmitate, linoleate, and linolenate contents and in increases in oleate and stearate contents. A dramatic effect on the quality of groat-oil in oat is not likely to occur with selection for increased groat-oil content.

Selection for Quantitative Traits in a Greenhouse

In plant breeding programs, selection for quantitative traits usually is based on data collected from field experiments. Greenhouses are utilized for increasing seed quantities, advancing generations, and intermating. The value of greenhouses for evaluating quantitative traits depends upon the magnitude of genotype-environment interaction that occurs between the field and greenhouse

environments. Studies by Youngs and Forsberg (1979), Thro and Frey (1985), and Gullord (1986) indicate that genotype-environment interaction for groat-oil content is small. Thus, selection for groat-oil content on the basis of data collected from greenhouse-grown oat plants in a recurrent selection program, might maximize the annual gain from selection.

Recent reports have shown that selection in greenhouses can be effective for some quantitatively inherited traits. Byrne and Rasmusson (1974) altered the ^{89}Sr content in wheat and barley by three cycles of bidirectional recurrent selection in the greenhouse. Crosbie et al. (1981) increased the CO_2-exchange rate of maize by utilizing two cycles of phenotypic recurrent selection per year, one cycle conducted in the field and one in the greenhouse. Both gridded mass selection in the field and selection within-HS families in the greenhouse increased the oil content in a recurrent selection program for soybean (Burton and Brim, 1981). Three cycles of recurrent selection in the greenhouse significantly decreased heading date of winter wheat (Avey et al., 1982).

Recurrent Selection in Small Grains

Recurrent selecton is a breeding method that is cyclical and repetitive and that is designed to gradually increase the frequency of favorable alleles of quantitatively inherited traits in plant populations (Hallauer, 1985). The improved

population can be a source of parent lines or new cultivars. Adequate genetic variability must be maintained in the plant population to permit continuous improvement of the mean for the trait under selection (Hallauer, 1981). A cycle of recurrent selection involves three phases: (1) development of progenies, (2) evaluation of progenies, and (3) recombination of superior progenies.

Various forms of recurrent selection have been used extensively in maize research (Hallauer and Miranda, 1988). Difficulties in intermating selected progenies and obtaining enough seed for replicated field experiments has limited the use of recurrent selection in autogamous crops. Several authors have made suggestions to overcome these limitations. For example, Gilmore (1964) outlined a procedure for using reciprocal recurrent selection utilizing either genetic or cytoplasmic male sterility to facilitate crossing in barley, wheat, and sorghum (Sorghum bicolor L.) with the ultimate goal to produce hybrids. Brim and Stuber (1973) outlined recurrent selection schemes for use with soybeans by utilizing a recessive genetic male-sterile allele. And Sorrels and Fritz (1982) proposed a recurrent selection scheme that uses a dominant male-sterile allele in wheat and cotton.

Jensen (1970) outlined the diallel selective mating system which provides for broad use of germplasm and utilizes recurrent selection. Jensen (1988) also suggested the use of

a male-sterile facilitated recurrent selection method in barley. With this method a population containing recessive male-sterile alleles is maintained in bulk. After several generations all F-stages will occur in the population, and head selection may begin.

Frey et al. (1988) developed a recurrent selection procedure for application in spring-sown small grains that utilizes: (1) the approach method of crossing (McDaniel et al., 1967), (2) early generation testing by evaluating $S_{0:1}$ lines, and (3) microplots for evaluation. In Iowa, one cycle of $S_{0:1}$ line recurrent selection can be completed each year by growing two generations in the greenhouse and one in the field.

Foroughi-Wehr and Wenzel (1990) outlined a procedure for introducing quantitative traits in currently grown barley cultivars by, what they call "recurrent selection alternated with haploid steps". Actually it is backcrossing alternated with haploid steps. Their procedure can, however, easily be modified for use in recurrent selection as follows: (1) production of crosses, (2) haploidization followed by diploidization of S_0's to develop large amounts of homozygous lines, (3) initial greenhouse screening for qualitatively inherited traits of the doubled haploids, (4) field evaluation of quantitatively inherited traits, and (5) intermating selected lines. Production of doubled haploids is done routinely in barley.

The number of reports on the use of recurrent selection in oat, wheat, and barley is limited. Byrne and Rasmusson (1974) reported that three cycles of bidirectional recurrent selection for ^{89}Sr content in wheat and barley grain gave progress in both directions in both crops. Selection was based upon data collected from greenhouse-grown F_3 progenies.

McNeal et al. (1978) increased grain protein content in spring wheat 25 g kg^{-1} after two cycles of F_3 line recurrent selection. Löffler et al. (1983) obtained an increase in protein content in hard red spring wheat grain of 5 g kg^{-1} $cycle^{-1}$ after two cycles of F_3 line recurrent selection. Three cycles of phenotypic recurrent selection in the greenhouse in winter wheat shifted the population mean towards earlier heading (Avey et al., 1982).

Busch and Kofold (1982) obtained a 7% increase in kernel weight of spring wheat after four cycles of individual S_1 plant recurrent selection. Patel et al. (1985) selected among doubled haploids produced from S_0's for one cycle of recurrent selection but found no increase in grain yield. Payne et al. (1986) obtained an increase in grain yield of 11.5% after three cycles of $F_{4:6}$ line recurrent selection in a population of oat. Bregitzer et al. (1987) evaluated the same recurrent selection program and showed a 13.5% gain in grain yield.

Two spring barley populations were used by Parlevliet and van Ommeren (1988a) for single F_2 plant followed by

F_3 line recurrent selection for partial resistance to barley leaf rust (Puccinia hordei) and powdery mildew (Erysiphe graminis f.sp. hordei). After three cycles average amounts of sporulating leaf tissue caused by barley leaf rust, was only 5% of that in the C_0. A four-fold increase was obtained for resistance against powdery mildew. Two cycles of recurrent selection for grain yield in the same two barley populations gave increases of 16.5% and 27.0% (Parlevliet and van Ommeren, 1989b). Both individual F_2 plant selection and F_3 line selection contributed to the increases.

A linear increase of 9.26 g kg^{-1} $cycle^{-1}$ in groat-oil content of oat was reported by Branson and Frey (1989a) after three cycles of phenotypic recurrent selection. McFerson and Frey (1990) applied the $S_{0:1}$ line recurrent selection procedure proposed by Frey et al. (1988) to increase protein yield of oat. Increases after three cycles were 21, 21, and 27 kg ha^{-1} $cycle^{-1}$ for three populations each subjected to a different selection strategy. Klein (1990) also utilized $S_{0:1}$ line recurrent selection and obtained, after three cycles of selection, increases in test weight of 6.9 and 17.8 kg m^{-3} $cycle^{-1}$ in two oat populations.

Genetic or cytoplasmic male sterility has not been utilized in any of the recurrent selection programs discussed in this section. In most studies, early generation testing was practised to reduce the cycle time. In all but one study, recurrent selection was successful.

Recurrent Selection for Oil Content

Recurrent selection to elevate seed-oil content has been successful with soybean, maize, and oat. Burton and Brim (1981) conducted three cycles of recurrent selection for high seed-oil content in a soybean population segregating for male sterility. Each cycle consisted of (1) intermating among male fertile and male-sterile plants, (2) selection for high seed-oil content among field-grown male-sterile plants, and (3) selection in the greenhouse within-HS families from selected male-sterile plants. After three cycles of selection an increase in seed-oil content of 3.5 g kg^{-1} $cycle^{-1}$ was obtained. Seed weight and seed-protein content decreased over cycles of selection. No correlated changes occurred for grain yield, oil and protein yield, total oil and protein content per seed, days to flowering, maturity, and lodging.

Seven cycles of within-HS family recurrent selection for kernel-oil content in a maize population, were conducted by Miller et al. (1981). Oil content increased 6.7 g kg^{-1} $cycle^{-1}$ and associated changes were reduced kernel weight and ear height and increased grain moisture. No changes occurred for grain yield, silking date, and plant height.

Misevic and Alexander (1989) conducted 24 cycles of phenotypic recurrent selection for percent oil in maize. During the first four cycles mass selection was practiced and

in the last 20 cycles intra-ear selection was used. Kernel-content in the population per se increased 4.9 g kg^{-1} $cycle^{-1}$, and the trait did not plateau. Grain yield decreased 71.6 kg ha^{-1} $cycle^{-1}$, and lodging, plant height, ear height, ear length, and kernel weight also decreased. Grain moisture and ear row number increased and silking date did not change. Oleate content increased and linoleate content decreased 1.39 g kg^{-1} $cycle^{-1}$.

Three cycles of phenotypic recurrent selection for high groat-oil content in oat were carried out by Branson and Frey (1989a). The original population was an A. sativa gene pool with A. sterilis alleles for high oil content introgressed into it. For each cycle, about 1000 field-grown S_0 plants were evaluated for groat-oil content and the highest 10% were selected and intermated. They obtained a linear increase of 9.26 g kg^{-1} $cycle^{-1}$ in groat-oil content and of 21 kg ha^{-1} $cycle^{-1}$ in oil yield. No associated changes occurred for heading date, plant height, biomass, grain yield, harvest index, groat yield, groat fraction, seed weight, and test weight (Branson and Frey, 1989b).

Explanation of Dissertation Format

This dissertation contains four sections that deal with three recurrent selection regimes for increasing groat-oil content in oat. In section I the genetic correlation between groat-oil contents of field- and greenhouse-grown oat plants

are estimated and for each of the three recurrent selection regimes genetic gains in groat-oil content are predicted. The actual gains in groat-oil content for the three regimes are evaluated in section II. In section III an evaluation is made to determine whether selection for groat-oil content via the three selection regimes caused any changes in agronomic traits. Finally, in section IV the effect of recurrent selection for increased groat-oil content upon the fatty acid composition is studied.

Each section is in the form of a complete manuscript that will be submitted for publication with little or no modification. Preceding the four sections are the general introduction and review of literature. The general summary, additional references, and acknowledgments follow after the sections.

SECTION I.

SELECTION FOR GROAT-OIL CONTENT IN OAT GROWN IN FIELD AND GREENHOUSE

ABSTRACT

Selection for quantitative traits of oat (Avena sativa L.) usually is based upon field experiments. The objective of this study was to determine whether a greenhouse could be utilized to select for greater groat-oil content in oat. Forty-eight oat lines from the C_0 to C_3 of a recurrent selection program to increase groat-oil content were evaluated in the field and greenhouse in 1987 and 1988. Groat-oil contents of large and small samples of oat groats were determined for each entry in each environment except for small samples from the greenhouse in 1987. The genetic correlation between groat-oil contents of field- and greenhouse-grown plants was 0.87, and between groat-oil contents of large and small samples it was 1.14. Estimates of heritabilities, variances, and genetic correlations were used to compute the predicted genetic gains, expressed under field conditions, from one cycle of each of three recurrent selection regimes. A regime that utilized selection among S_0 plants in the field followed by selection among and within selected $S_{0:1}$ progenies in the greenhouse, gave annual predicted gains in groat-oil content that were 38% and 186% greater than predicted gains from phenotypic recurrent selection regimes with selection among field- and greenhouse-grown S_0 plants, respectively. Thus, selection for groat-oil content in oat on the basis of data from the greenhouse can

be successfully incorporated into a recurrent selection program.

INTRODUCTION

In cereal breeding programs, selection for quantitative traits usually is based on data collected from field experiments. Environments represented by off-season nurseries in the tropics or greenhouses are utilized for increasing seed quantities, advancing generations, and intermating; but seldom are they used for selection. Recent reports indicate that selection in off-season environments can be effective for some characteristics. Cianzio (1985) showed that selection for specific seed composition of soybean [Glycine max (L.) Merr.] genotypes adapted to the Cornbelt was effective when data from winter nurseries in Puerto Rico were utilized. Crosbie et al. (1981) increased the CO_2-exchange rate of maize (Zea mays L.) by using two two cycles of phenotypic recurrent selection per year, one cycle conducted in the field and one in the greenhouse. Burton and Brim (1981) showed that both gridded mass selection in the field and selection within-HS families in the greenhouse increased the oil content in a recurrent selection program for soybean. Avey et al. (1982) used three cycles of recurrent selection in the greenhouse to significantly decrease heading date of winter wheat (Triticum aestivum L.).

The value of off-season nurseries and greenhouses for selecting quantitative traits largely depends upon the

magnitude of genotype-environment (GE) interaction that occurs between the field environments and the greenhouse or off-season nurseries. Analysis of GE interaction, however, does not predict the best selection environment, and normally GE interaction variance cannot be subdivided to give a portion due to rank change among genotypes, which is of paramount importance (Comstock, 1977).

Falconer (1952) suggested a model to study GE interaction whereby the expressions of a trait in two environments are regarded as two traits. Parameters in his model are heritabilities of the trait in the two environments and the genetic correlation (r_G) between the trait values from the two environments. The r_G measures the degree to which the trait is determined by the same sets of genes in the two environments, and a low r_G generally reflects a large GE interaction. The Falconer model was used by Frey (1965) to show that hill plots would accurately evaluate yield, plant height, and test weight of oat lines. Weaver and Wilcox (1982) used it to show that the genetic correlations for several traits of soybean were near unity when evaluated at different row spacings. The r_G between soybean yields from early and late plantings were not different from unity in a study by Pfeiffer (1987). Lambert (1984) obtained genetic correlations ranging from 0.02 to 0.87 between maize yields from high and normal productivity environments. Atlin and Frey (1990) found that r_G between grain yields of 116 oat

lines tested in low- and high-productivity environments was 0.59, which led them to conclude that yields of oat in the two environments were controlled by substantially different sets of genes.

Recently, a considerable increase in groat-oil content of oat has been accomplished (Branson and Frey, 1989). Oat with higher groat-oil contents might be more profitable as a high-energy feed grain or as a possible source of high quality culinary oil (Frey and Hammond, 1975). Thro and Frey (1985), Guilord (1986), and Branson and Frey (1989) have shown that the GE interaction for groat-oil content of oat is small and usually not significant. Further, Baker and McKenzie (1972), Brown et al. (1974), and Branson and Frey (1989) found that heritabilities of groat-oil content of oat ranged from 0.63 to 0.93. Frey et al. (1975) showed that the inheritance of groat-oil content in oat is quantitative with high oil content being partially dominant, and Thro and Frey (1985) found that gene action determining groat-oil content was primarily additive. Neither dominance nor epistatic gene action was significant.

The objectives were: (1) to estimate heritabilities and GE interactions for groat-oil content in field- and greenhouse-grown oat plants, (2) to estimate genetic correlations between groat-oil contents of field- and greenhouse-grown oat plants and between groat-oil contents of large and small groat samples, and (3) to predict gains in

groat-oil content from three recurrent selection regimes, two of which utilize greenhouse selection.

MATERIALS AND METHODS

Materials

The materials for this study were 39 random $S_{0:3}$ (S_0-derived line in S_3) oat lines from the C_0 to C_2 and nine random $S_{0:2}$ lines from the C_3 of a recurrent selection program for increasing groat-oil content of oat (Branson and Frey, 1989). Groat-oil content of these lines ranged from 72.4 to 126.7 g kg^{-1}.

Environments

During the summers of 1987 and 1988, the 48 oat lines were evaluated in randomized complete-block designs at the Agronomy and Agricultural Engineering Field Research Center near Ames, Iowa, and in the Agronomy Greenhouse in Ames. Each experiment had two replications. Before planting, field experimental areas received broadcast applications of 34, 22, and 28 kg ha^{-1} of N, P, and K, respectively. A field plot was a 3 m row, and plots were spaced 90 cm apart. Ten seeds were space-sown 30 cm apart within a plot, and the plots were thinned to six plants at the two-leaf stage. Seedlings were sprayed with an insecticide at the one-leaf stage and at weekly intervals thereafter to kill aphids that transmit the barley yellow dwarf virus. At maturity, the plants in a plot were harvested and threshed in bulk.

In the greenhouse, a plot consisted of three pots sown

with four seeds each and thinned to two seedlings at the two-leaf stage. Temperature and day length regimes were 21°C day/18°C night and 9 h, respectively, for 5 wk post-emergence and then 23°C day/18°C night and 15 h, respectively, until maturity. The growth medium was a mixture of peat, loam (Iowa soil), and sand mixed in a 4:4:2 ratio. Perlite was added to aid aeration. Plots were watered as needed, and solutions of N, P, and K were applied weekly. Plants were sprayed with insecticides and fungicides as needed. When mature, the plants from a plot were harvested and threshed in bulk.

A sample of oat seeds from each field and greenhouse plot from 1987 and 1988 was dehulled to obtain 3.5 to 6.0 g of groats (large samples). Additionally, for each plot from the field experiments and from the greenhouse experiment in 1988, a sample of 13 seeds was dehulled (small samples). The groat samples were analyzed for oil content by the wide-line nuclear magnetic resonance (NMR) method described by Conway and Earle (1963).

Statistical Analyses

An analysis of variance was computed for each sample size over years within each location; i.e., field and greenhouse. Variance components due to genotypes (σ^2_G), and genotype-year interactions (σ^2_{GY}) were estimated as linear functions of the appropriate mean squares. Further, for

large samples, variance components due to genotypes and genotype-location interactions (σ^2_{GL}) were obtained from the combined analysis over years and locations. Genotypes and years were considered to be random effects and locations to be fixed. Approximate 90% confidence intervals for variance components were calculated by using the method of Bulmer (1957). Negative variance estimates were assumed to be zero.

Heritabilities for groat-oil content from large and small groat samples from field- and greenhouse-grown plants were calculated on an entry mean basis by using the formula:

$$H^2 = \hat{\sigma}^2_G / (\hat{\sigma}^2_G + \hat{\sigma}^2_{GY}/y + \hat{\sigma}^2/ry)$$

where y and r are number of years and replications, respectively. Exact 90% confidence intervals for H^2 were calculated by using the method of Knapp et al. (1985).

The genetic correlations between groat-oil contents of large samples from field- and greenhouse-grown plants and between groat-oil contents from large and small samples from field-grown plants were computed by using the formula:

$$r_G = \hat{\sigma}_G / (\hat{\sigma}_{G(a)}\ \hat{\sigma}_{G(b)})$$

where $\hat{\sigma}_G$ is the genetic covariance for the two measurements of groat-oil content and $\hat{\sigma}_{G(a)}$ and $\hat{\sigma}_{G(b)}$ are the genetic standard deviations of the two measurements. Approximate standard errors for the correlations were calculated by using the method of Falconer (1981).

Predicting Genetic Gains from Selection

Using data from large samples, the predicted response (R) from selection for groat-oil content in the field and the correlated response (CR) in the field to indirect selection in the greenhouse, were calculated according to formulas from Falconer (1981):

$$R = i\ H_f\ \hat{\sigma}_{G(f)} \quad \text{and}$$

$$CR = i\ H_{gh}\ H_f\ r_G\ \hat{\sigma}_{P(f)}$$

where i is the standardized selection differential, H_{gh} and H_f are the square roots of heritability in greenhouse and field, respectively, $\hat{\sigma}_{G(f)}$ and $\hat{\sigma}_{P(f)}$ are the genetic and phenotypic standard deviations of groat-oil content based upon large samples in the field, and r_G is the genetic correlation between groat-oil contents in the field and in the greenhouse. By rearranging the R and CR equations and using equal standardized selection differentials the ratio CR/R is obtained:

$$CR/R = r_G\ (H_{gh}/H_f)$$

Utilizing data from field-grown plants, the same formulas were used to calculate response from selection for groat-oil content based upon large samples, the correlated response in large samples to indirect selection based upon small samples, and the CR/R ratio by substituting the appropriate heritabilities, variances, and genetic correlation.

Predicted genetic gains were calculated for three

recurrent selection regimes: (1) Phenotypic recurrent selection among S_0 plants in the field followed by intercrossing selected $S_{0:1}$ lines in the greenhouse. This regime requires two generations per cycle and one cycle could be accomplished in one year. (2) The same as in (1) except that all selections and intermatings are done in the greenhouse. Three generations can be obtained per year so 1.5 cycles can be conducted each year. (3) Phenotypic recurrent selection among S_0 plants in the field followed by selection in the greenhouse among and within $S_{0:1}$ progenies from selected S_0 plants during September to December. Intermatings are made among $S_{1:2}$ lines from selected S_1 plants during December to March in the greenhouse. This regime requires three generations per cycle, one in the field and two in the greenhouse, and one cycle can be completed in one year. Frey et al. (1988) described the protocol for producing three crops of oat in a year.

Predicted genetic gains in groat-oil content of oat for the three regimes of recurrent selection were computed by using (Eberhart, 1970):

$$\Delta G = (i \; c \; \hat{\sigma}^2_A) \; / \; \hat{\sigma}_P$$

in which i is the standardized selection differential, c is the coefficient of additive variance (which equals 1.0 for selection among S_0 plants and $S_{0:1}$ progenies and 0.5 for selection among plants within $S_{0:1}$ progenies), $\hat{\sigma}^2_A$ is the additive variance, and $\hat{\sigma}_P = \sqrt{(\hat{\sigma}^2 + \hat{\sigma}^2_{GY} + \hat{\sigma}^2_G)}$ for selection

among S_0 plants and among $S_{0:1}$ progenies and $\hat{\sigma}_P = \sqrt{(\hat{\sigma}^2 + \frac{1}{2}\hat{\sigma}^2_{GY} + \frac{1}{2}\hat{\sigma}^2_G)}$ for selection among plants within $S_{0:1}$ progenies. The values for i were obtained from tables presented by Becker (1984). It was assumed that no dominance or epistatic gene action occur in the determination of groat-oil content of oat. Predicted gains from selection in the greenhouse were multiplied by the appropriate CR/R ratio(s) to obtain predicted gains in groat-oil content when evaluated in the field and when large samples are used.

To calculate predicted genetic gains, estimated parameters from large samples were used for field-grown plants, and estimated parameters from small samples were used for greenhouse-grown plants because only small amounts of seed can be obtained from plants grown in a greenhouse. Predicted genetic gains were computed for initial population sizes N_I=300 and N_I=1000.

RESULTS AND DISCUSSION

Groat-oil content of oat was significantly less for greenhouse-grown than for field-grown seeds (Table 1). Further, small samples gave greater means for groat-oil content than did large ones. The 2-yr mean for both large and small samples was 21% greater for field- than for greenhouse-grown seeds. The discrepancy in groat-oil contents of large and small samples probably was due to procedural differences in the NMR analyses. The phenotypic correlation between groat-oil contents from large and small samples was 0.90 ($p \leq 0.01$), which shows that the rankings of genotypes were similar for both sample sizes. Thus, either sample size could be used when breeding oat for high groat-oil content.

When analyzed within and across locations the mean squares for genotypes were significant. Genotype-year interactions were not significant (analyses not shown). Therefore, selection for groat-oil content can be based on data for a single year with confidence of selecting the correct genotypes. The year effect on groat-oil content was large for both sample types (27.2 g kg^{-1} with large samples from field-grown materials), but unidirectional. The interaction of genotypes, years, and locations was not significant, but the genotype-location interaction was significant ($p \leq 0.05$). This latter interaction occurred

Table 1. Means of groat-oil content for large and small samples of 48 oat lines tested in two locations in 1987 and 1988

Location	Large samples			Small samples	
	1987	1988	Mean	1987	1988
	g kg^{-1}			g kg^{-1}	
Field	77.2*	104.4*	90.8*	98.3	114.1*
Greenhouse	73.8	76.3	75.0	-	94.2
Mean	75.5	90.3		-	104.3

*Means for field and greenhouse are significantly different at the 0.05 probability level.

because the year effect on groat-oil content was much larger in the field than in the greenhouse. The phenotypic correlation between groat-oil contents of 1987 and 1988 field-grown samples of genotypes was 0.75 ($p \leq 0.01$), and between field and greenhouse materials, the correlation was 0.70 ($p \leq 0.05$). This indicates that the rankings of genotypes for groat-oil content were similar in different years and locations.

The 90% confidence intervals for the genetic variances for groat-oil contents of large and small samples from field and greenhouse overlapped, thus the estimates from the two locations were not significantly different (Table 2). Further, the genotype-year interaction was not significant in the field or greenhouse, and the ratios of genetic variance to error variance were similar in magnitude at both locations for large and for small samples. These results also suggest

Table 2. Variance components and heritabilities with confidence intervals for groat-oil content evaluated on large and small samples of field- and greenhouse-grown oat lines

Component	Field	Greenhouse
	Large samples	
$\hat{\sigma}^2_G$	52.5 (35.9, 81.9)[a]	33.5 (22.3, 52.1)
$\hat{\sigma}^2_{GY}$	-1.3 (-9.7, 8.5)	2.5 (-2.7, 9.3)
$\hat{\sigma}^2$	41.6	23.3
H^2	0.83 (0.75, 0.89)	0.83 (0.72, 0.89)
	Small samples	
$\hat{\sigma}^2_G$	23.1 (14.0, 48.7)	24.4 (2.7, 52.1)
$\hat{\sigma}^2_{GY}$	-9.5 (-26.6, 8.0)	-[b]
$\hat{\sigma}^2$	86.1	66.8
H^2	0.52 (0.28, 0.69)	0.42 (0.06, 0.65)

[a]Values in parentheses indicate 90% confidence limits.

[b]Data from only 1 year available.

that response to selection for groat-oil content of oat would be similar in the field and greenhouse when based on equal sample sizes.

Broad-sense heritability for groat-oil content of oat was 0.83 for both field- and greenhouse-grown plants when large groat samples were analyzed. These heritability values agree with previous reports (Baker and McKenzie, 1972; Brown et al., 1974; Branson and Frey, 1989). Heritability of

groat-oil content based upon small samples was significantly lower than that based upon large samples, which suggests that selection based upon small samples would be less effective than selection based upon large ones.

The genetic correlation between groat-oil contents from the field and greenhouse based upon large samples was 0.87±0.04. Because the heritabilities from field and greenhouse were identical (0.83), the CR/R ratio is equivalent to r_G or 0.87. That is, gain in groat-oil content from selection in the greenhouse based upon large samples would be 87% of that obtained from selection in the field. Another interpretation would be that groat-oil contents in the field and in the greenhouse are determined largely by the same set of genes. The high value of r_G, the equal heritabilities in field and greenhouse, and the high CR/R ratio all indicate that selection for groat-oil content of oat in the greenhouse should be effective when based upon large samples. The genetic correlation between groat-oil contents from large and small samples utilizing field-grown plants was 1.14±0.07, and the corresponding CR/R ratio was 0.79. By multiplying the CR/R ratios for greenhouse vs. field and large vs. small samples (i.e., 0.87 x 0.79), the resulting product is 0.68, which means that gain in groat-oil content from selection in the greenhouse based on small samples would be 68% as effective as selecting in the field on the basis of large samples.

The predicted gains in groat-oil content per year from recurrent selection regime 1 was 9.45 and 9.50 g kg^{-1} for initial population sizes (N_i) of 300 and 1000 plants, respectively (Table 3). The predicted gains for regimes 2 and 3 were 4.57 and 11.58 g kg^{-1}, respectively, for N_i=300 and 4.60 and 13.14 g kg^{-1}, respectively, for N_i=1000. Regime 1 with N_i=1000 was the procedure used by Branson and Frey (1989), and they obtained an increase of 9.26 g kg^{-1} in groat-oil content per cycle over three cycles, which is similar to the predicted gain of 9.50 g kg^{-1}. For regime 3, which involved two phases of selection and one intercrossing per cycle, the predicted annual gain for N_i=300 was 11.58 g kg^{-1}, which was 23% and 153% greater than the annual gains for regimes 1 and 2. When N_i=1000, the predicted annual gain for regime 3 was 38% and 186% greater than gains for regimes 1 and 2, respectively. Increasing N_i from 300 to 1000 elevated the annual genetic gain in groat-oil content for both regimes 1 and 2 by only 0.5%. By making a similar increase in N_i for regime 3, however, the standardized selection differentials for selection among and within $S_{0:1}$ progenies could be increased substantially, resulting in a 13.4% greater genetic gain. By increasing the N_i from 300 to 1000 for regimes 1 and 2, the number of selected lines is increased from 30 to 100 for intermating to produce the next generation. For regime 3, only 30 lines are selected in each cycle, so this regime should encounter

Table 3. Predicted genetic gains for groat-oil content of oat expressed under field conditions per cycle (ΔG_c) and per year (ΔG_y) for three recurrent selection regimes and two initial population sizes (N_i)

Regime		N[a]	n[b]	i[c]	ΔG_c	ΔG_y
					— g kg^{-1} —	
		N_i=300				
1. field		300	30	1.746	9.45	9.45
2. greenhouse		300	30	1.746	3.05	4.57
3. field		300	30	1.746	9.45	
greenhouse:	among	30	24	0.338	0.59	11.58
	within	240	30	1.647	1.55	
		N_i=1000				
1. field		1000	100	1.755	9.50	9.50
2. greenhouse		1000	100	1.755	3.07	4.60
3. field		1000	100	1.755	9.50	
greenhouse:	among	100	30	1.149	2.01	13.14
	within	300	30	1.746	1.64	

[a] N = population size.

[b] n = number of plants or progenies selected.

[c] i = standardized selection differential.

negative effects from inbreeding sooner.

Phenotypic recurrent selection carried out entirely in the greenhouse (regime 2) is less effective than regime 1 for increasing groat-oil content of oat on an annual basis. Moreover, the work involved each year is greater for regime 2 than for regime 1. Thus, regime 2 is more costly per unit of increase of groat-oil content. Adding a second generation in the greenhouse for selection among S_1 plants within selected

$S_{0:1}$ lines (regime 3) was effective for obtaining greater gain per year. The cost of growing and evaluating an extra 1000 plants in the greenhouse would be small for the 38% greater predicted gain per year than for regime 1.

The results suggest that phenotypic recurrent selection among S_0 plants in the field, followed by additional selection among greenhouse-grown $S_{0:1}$ progenies from selected S_0 plants and among S_1 plants within selected $S_{0:1}$ progenies, is a regime that can significantly increase the gain per year in groat-oil content of oat.

REFERENCES

Atlin, G.N., and K.J. Frey. 1990. Selecting oat lines for yield in low-productivity environments. Crop Sci. 30: 556-561.

Avey, D.P., H.W. Ohm, F.L. Patterson, and W.E. Nyquist. 1982. Three cycles of simple recurrent selection for early heading in winter wheat. Crop Sci. 22:908-912.

Baker, R.J., and R.I.H. McKenzie. 1972. Heritability of oil content in oats, Avena sativa L. Crop Sci. 12:201-202.

Becker, W.A. 1984. Manual of quantitative genetics. 4th ed. Academic Enterprises, Pullman, WA.

Branson, C.V., and K.J. Frey. 1989. Recurrent selection for groat oil content in oat. Crop Sci. 29:1382-1387.

Brown, C.M., A.N. Aryeetey, and S.N. Dubey. 1974. Inheritance and combining ability for oil content in oats (Avena sativa L.). Crop Sci. 14:67-69.

Bulmer, M.G. 1957. Approximate confidence limits for components of variance. Biometrika 44:159-167.

Burton, J.W., and C.A. Brim. 1981. Recurrent selection in soybeans. III. Selection for increased percent oil in seeds. Crop Sci. 21:31-34.

Cianzio, S.R. de. 1985. Off-season nurseries enhance soybean breeding and genetics programs. p. 329-336. In R. Shibles (ed.) World Soybean Res. Conf. III: Proc. Ames, IA. 12-17 Aug. 1984. Westview Press, Boulder, CO and London, England.

Comstock, R.E. 1977. Quantitative genetics and the design of breeding programs. p. 705-718. In E. Pollak et al. (ed.) Proc. Int. Conf. Quant. Genet. Ames, IA. 16-21 Aug. 1976. Iowa State Univ. Press, Ames, IA.

Conway, T.F., and F.R. Earle. 1963. Nuclear magnetic resonance for determining oil content of seeds. J. Am. Oil Chem. Soc. 40:265-268.

Crosbie, T.M., R.B. Pearce, and J.J. Mock. 1981. Recurrent phenotypic selection for high and low photosynthesis in two maize populations. Crop Sci. 21:736-740.

Eberhart, S.A. 1970. Factors effecting efficiencies of breeding methods. African Soils 15:669-680.

Falconer, D.S. 1952. The problem of environment and selection. Am. Nat. 86:293-298.

Falconer, D.S. 1981. Introduction to quantitative genetics. 2nd ed. Longman, London, England.

Frey, K.J. 1965. The utility of hill plots in oat research. Euphytica 14:196-208.

Frey, K.J., and E.G. Hammond. 1975. Genetics, characteristics, and utilization of oil in caryopses of oat species. J. Am. Oil Chem. Soc. 52:358-362.

Frey, K.J., E.G. Hammond, and P.K. Lawrence. 1975. Inheritance of oil percentage in interspecific crosses of hexaploid oats. Crop Sci. 15:94-95.

Frey, K.J., J.K. McFerson, and C.V. Branson. 1988. A procedure for one cycle of recurrent selection per year with spring-sown small grains. Crop Sci. 28:855-856.

Gullord, M. 1986. Oil and protein content in oats (Avena sativa L.). p. 210-213. In D.A. Lawes and H. Thomas (ed.) Proc. 2nd Int. Oats Conf. Aberystwyth, Wales. 15-18 July 1985. Martinus Nijhoff Publishers, Dordrecht, The Netherlands.

Knapp, S.J., W.W. Stroup, and W.M. Ross. 1985. Exact confidence intervals for heritability on a progeny mean basis. Crop Sci. 25:192-194.

Lambert, R.J. 1984. Reciprocal recurrent selection of maize in a high-yield environment. Maydica 29:419-430.

Pfeiffer, T.W. 1987. Selection for late-planted soybean yield in full-season and late-planted environments. Crop Sci. 27:963-967.

Thro, A.M., and K.J. Frey. 1985. Inheritance of groat-oil content and high-oil selection in oats (Avena sativa L.). Euphytica 34:251-263.

Weaver, D.B., and J.R. Wilcox. 1982. Heritabilities, gains from selection, and genetic correlations for characteristics of soybeans grown in two row spacings. Crop Sci. 22:625-629.

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SECTION II.

THREE RECURRENT SELECTION REGIMES TO INCREASE GROAT-OIL CONTENT OF OAT

ABSTRACT

Three recurrent selection regimes were evaluated to measure the response of selection for groat-oil content (GO) of oat (Avena sativa L.) in greenhouse- and field-grown plants. For regime 1, selection for GO occurred among S_0 plants grown in the field; for regime 2, selection occurred among S_0 plants grown in the greenhouse; and for regime 3, selection among field-grown S_0 plants was followed by selection among and within $S_{0:1}$ progenies grown in the greenhouse. Gains from selection for GO via the three regimes were evaluated by using random lines from each selection cycle of each regime. Groat-oil contents increased significantly in regimes 1 and 3 but not in regime 2. Annual gains in GO were 6.04, 5.85, and 11.98 g kg^{-1} in regimes 1, 2, and 3, respectively. Both selection among S_0 plants in the field and among and within $S_{0:1}$ progenies in the greenhouse contributed to the increased GO in regime 3. In each regime, the genetic variance of GO remained significant. Line M022-4-5 with a mean GO of 162.85 g kg^{-1} was the highest in GO in the evaluation experiment. Selection for GO on the basis of data from greenhouse-grown oat plants can be successfully incorporated into a recurrent selection program.

INTRODUCTION

Recurrent selection is a plant breeding procedure designed to change gradually the mean of a trait in a population of plants by increasing the frequency of favorable alleles. The procedure is especially suited for improving quantitatively inherited traits of plants, and it provides populations with high percentages of superior genotypes that can be useful as parents in breeding programs or as potential cultivars (Hallauer, 1985).

Difficulty in making crosses among selected lines and in obtaining enough seed for replicated evaluation experiments has limited the use of recurrent selection for oat. However, Frey et al. (1988) developed a recurrent selection strategy that overcomes these limitations. This strategy, which uses the approach method of crossing (McDaniel et al., 1967), early generation testing, and microplots for evaluation (Frey, 1965), allows for one cycle of $S_{0:1}$ line recurrent selection per year. McFerson and Frey (1990) and Klein (1990) utilized this strategy to successfully increase protein yield and test weight of oat, respectively.

Oil content of groats (caryopses) of oat is quantitatively inherited, with high groat-oil content being partially dominant (Frey et al., 1975). Thro and Frey (1985) reported that gene action was primarily additive and that neither dominance nor epistasis was important in determining

groat-oil content. Heritabilities of this trait generally are high, ranging from 0.63 to 0.93 (Baker and McKenzie, 1972; Brown et al., 1974; Branson and Frey, 1989). Genotype-environment interaction for groat-oil content is of minor importance (Thro and Frey, 1984; Gullord, 1986; Branson and Frey, 1989).

Oat has the highest groat-oil content of temperate cereals (Price and Parsons, 1975). Because of its relatively low linolenate and high oleate and linoleate contents, oat oil is of good culinary quality (Kalbasi-Ashtari and Hammond, 1977), and oat grain with high groat-oil content would be a high-energy feed grain. Frey and Hammond (1975) estimated that a groat-oil content of 160 g kg^{-1} would make oil extraction economical. Using phenotypic recurrent selection, Branson and Frey (1989) obtained an increase of 9.26 g kg^{-1} $cycle^{-1}$ in groat-oil content of oat. Mean groat-oil content of their C_3 population was 113.30 g kg^{-1}.

Quantitative traits usually cannot be successfully evaluated on greenhouse-grown plants. However, Burton and Brim (1981) increased seed-oil content of soybean [Glycine max (L.) Merr.] by utilizing selection in the field and in a greenhouse. Mass selection in the field followed by within-HS family selection in the greenhouse resulted in an increase of 3.5 g kg^{-1} $cycle^{-1}$ in seed-oil content. Schipper (1991) showed that selection for groat-oil content among greenhouse-grown oat plants can be successful.

The objectives were to evaluate the gains in groat-oil content of oat when using three recurrent selection regimes: (1) Phenotypic recurrent selection among S_0 plants in the field and intermating selected $S_{0:1}$ lines in the greenhouse; (2) Same as in (1) except that evaluating, selecting, and intermating is done in the greenhouse; and (3) Phenotypic recurrent selection among S_0 plants grown in the field followed by selection among and within $S_{0:1}$ progenies from selected S_0 plants in the greenhouse and intermating selected $S_{1:2}$ lines also in the greenhouse.

MATERIALS AND METHODS

Genepool Development and Selection Procedures

To develop the base population (C_0) for this study, eight high-oil A. sativa cultivars were crossed to eight high-oil A. sterilis accessions. These single cross F_1's were mated to eight A. sativa cultivars that had good agronomic characteristics to provide three-way matings. Selection for agronomic type and high groat-oil content was practiced among S_1 plants from the three-way matings, and selected S_1-derived lines were intercrossed. Next, S_0 plants from this intermating were selected for agronomic traits and high groat-oil content, and their progenies were randomly crossed to five other A. sativa cultivars. The S_0 plants from these latter crosses were intermated to provide seeds for the C_0. Development of the gene pool is described in detail by Branson and Frey (1989).

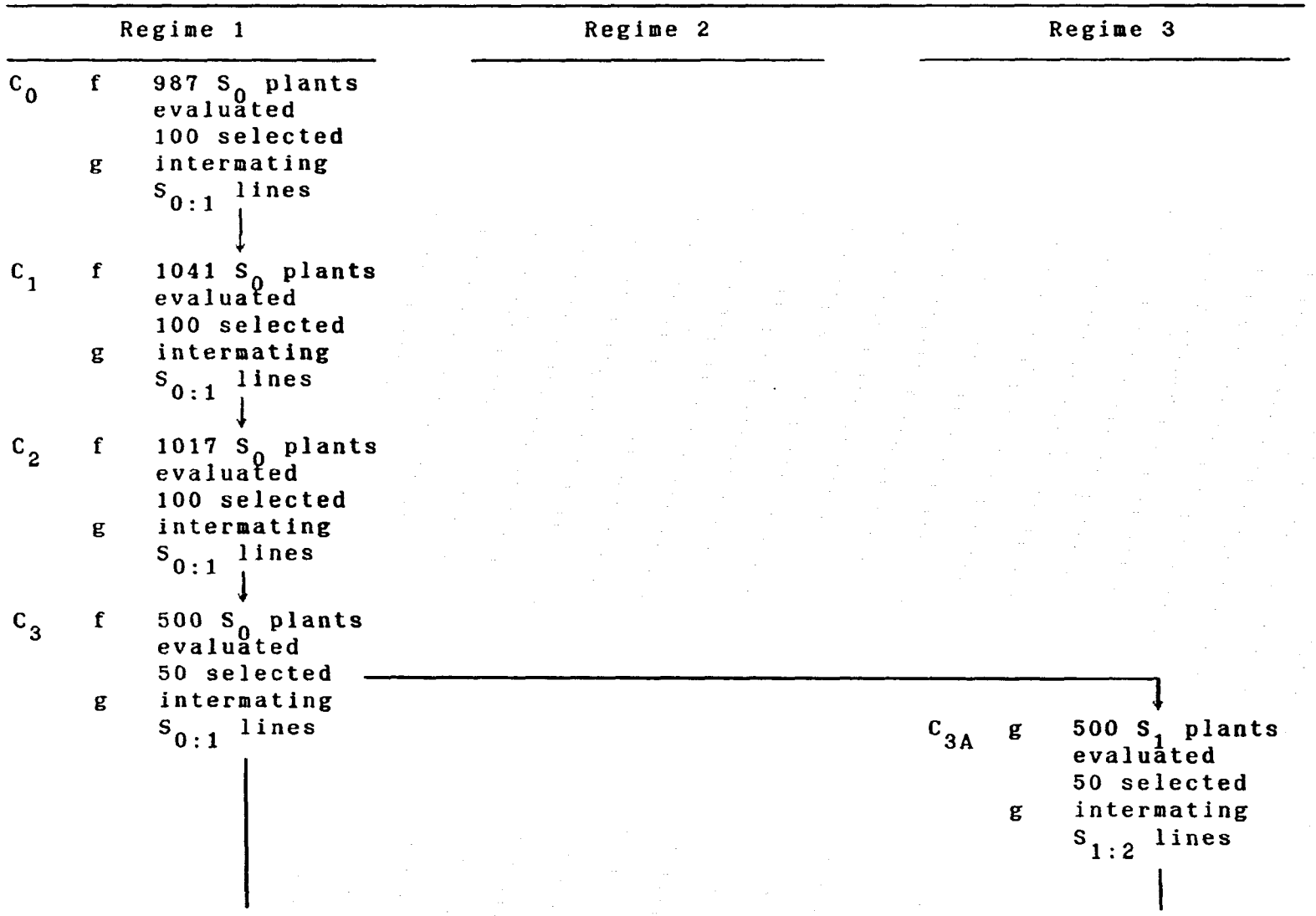
Recurrent selection regime 1 was initiated in 1983. Ca. 3500 S_0 seeds of the C_0 were space-sown in rows spaced 90 cm apart in the field. Each row was 3 m long and contained a FS progeny. The plants were grown at the Agronomy and Agricultural Engineering Field Research Center near Ames, Iowa, on a Nicollet silty loam (fine-loamy, mixed, mesic Aquic Hapludoll). Before planting the experimental area received a broadcast application of 34, 22, and 28 kg ha^{-1} of N, P, and K, respectively. At emergence and at weekly

intervals thereafter, plants were sprayed with an insecticide to kill aphids that transmit the barley yellow dwarf virus.

Visual selection was practiced among S_0 plants for desirable height and maturity, lodging resistance, seed and panicle type, and plant vigor. About 1000 S_0 plants were harvested, and a sample of seeds was dehulled from each to provide 3.5 to 6.0 g of groats for groat-oil analysis by wide-line nuclear magnetic resonance (NMR) spectroscopy (Conway and Earle, 1963). The 100 S_0 plants ranking highest in groat-oil content were selected, except that only one plant was chosen from any FS family. During winter, the selected $S_{0:1}$ lines were intermated with each line being crossed to four others. The goal was to obtain 10 S_0 seeds per cross for the first cycle of recurrent selection (C_1).

One year was used to complete a cycle of regime 1. The procedure was repeated six times (Fig. 1), except that only 500 plants were evaluated for groat-oil content in C_3, from which 50 were selected for intermating. Each $S_{0:1}$ line was mated to three others. Further, in the C_4, C_5, and C_6, groat-oil was measured on about 400 S_0 plants, and 30 $S_{0:1}$ lines were selected and intermated.

Regime 2 was begun in 1987. Procedures were similar to those of regime 1 except that all selections and intermatings were done in the greenhouse. The 30 selected S_0 plants of the C_4 of regime 1 were intermated and the S_0 seeds were sown in the greenhouse. Three S_0 plants were grown per pot in a


Regime 1
Regime 2
Regime 3
C0 f 987 S0 plants evaluated 100 selected g intermating S0:1 lines
C1 f 1041 S0 plants evaluated 100 selected g intermating S0:1 lines
C2 f 1017 S0 plants evaluated 100 selected g intermating S0:1 lines
C3 f 500 S0 plants evaluated 50 selected g intermating S0:1 lines
C3A g 500 S1 plants evaluated 50 selected g intermating S1:2 lines

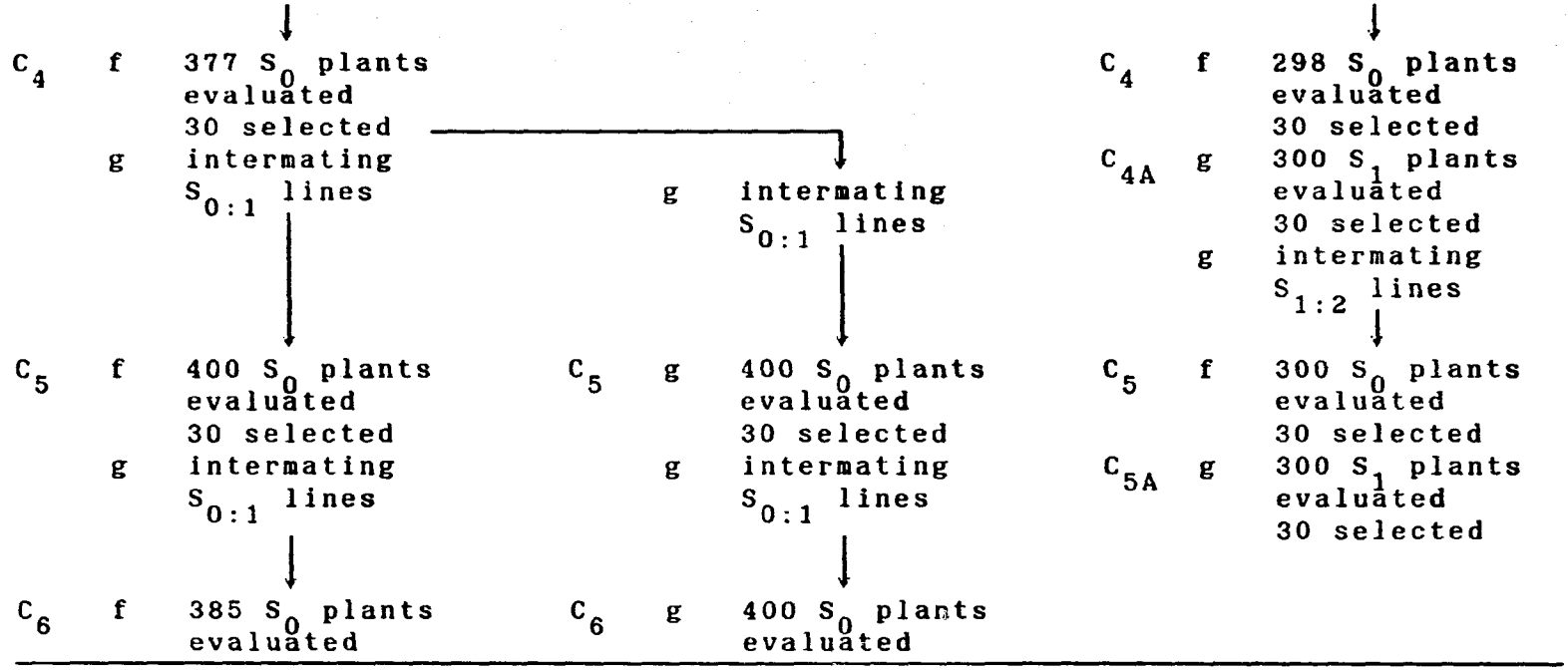


Figure 1. Flow chart of recurrent selection regimes 1, 2, and 3 (f or g indicate field- and greenhouse-grown, respectively)

mixture of peat, loam (Iowa soil), and sand used in a 4:4:2 ratio. Perlite was added to the medium to aid aeration. Plots were watered as needed, and solutions of N, P, and K were applied weekly. Plants were sprayed with insecticides and fungicides as needed. Temperature and day length regimes were 21°C day/18°C night and 9 h, respectively, for 5 wk post emergence and then 23°C day/18°C night and 15 h, respectively until maturity. From 400 S_0 plants, 13-seed samples were dehulled for NMR spectroscopy analyses, and 30 $S_{0:1}$ lines were selected and intermated to construct the C_5 population. This regime allowed for 1.5 cycles of recurrent selection per year, and two cycles were completed (Fig. 1).

Regime 3 was initiated in 1986. In September, 10 S_1 seeds from each of the 50 selected S_0 plants of the C_3 of regime 1 were sown in the greenhouse. This population of 500 S_1 plants was called C_{3A} (Fig. 1). Two plants were grown per pot, and pots were randomized on the bench. The environmental conditions were similar to those described for regime 2. At maturity, the S_1 plants were harvested individually, and from each, a 13-seed sample was dehulled and analyzed for groat-oil content. The mean groat-oil content was computed for the 10 S_1 plants from each $S_{0:1}$ line, and the 20% of $S_{0:1}$ lines with the lowest means were discarded. Among the remaining S_1 plants, 50 with the highest groat-oil content were selected and intermated during December to March in the greenhouse. Each $S_{1:2}$ line

was crossed to three others, and the goal was to obtain 10 S_0 seeds per cross. S_0 seeds of C_4, were space-sown in the the field as described for regime 1. The procedure was repeated for the fourth and fifth cycles of selection, except that only 300 field-grown S_0 plants were evaluated and only only 30 S_0 plants were selected (Fig. 1). The C_{4A} and C_{5A} consisted of 300 S_1 plants, and only 30 were selected. One cycle of recurrent selection of this regime was completed per year.

Evaluation Experiment

The efficacies of regimes 1, 2, and 3 of recurrent selection for increasing groat-oil content were evaluated in 1989. The evaluation experiment contained 100 random lines from each cycle of selection of each regime (Table 1). All selected lines also were evaluated except that for the C_0, C_1, and C_2 of regime 1, only half of the selected lines were evaluated. Sixteen of the 29 original parents (Y22-15-9, Pettis, Lang, D2263032, Dal, Stout, Wright, IL75-5743, Y341-41, Otee, Spear, Mo-06195, Orbit, Lodi, Nya-11, and Hazel) and four checks (Starter, Webster, Hamilton, and Ogle) were entered in the experiment twice each. Thus, there were 1900 entries in the evaluation experiment that was grown in a randomized complete-block design with two replications at each of two locations in Iowa: the Agronomy and Agricultural Engineering Field Research Center near Ames and the Northeast

Table 1. Numbers and stages of oat lines evaluated for regimes 1, 2, and 3

Cycle	Random		Selected	
	Lines	Stages	Lines	Stages
		Regime 1		
0	100	$S_{0:3}$	50	$S_{0:3}$
1	100	$S_{0:3}$	50	$S_{0:3}$
2	100	$S_{0:3}$	50	$S_{0:3}$
3	100	$S_{0:2}$	50	$S_{0:2}$
4	100	$S_{0:2}$	30	$S_{0:2}$
5	100	$S_{0:2}$	30	$S_{0:2}$
6	100	$S_{0:1}$		
		Regime 2		
5	100	$S_{0:2}$	30	$S_{0:2}$
6	100	$S_{0:1}$		
		Regime 3		
3A	100	$S_{1:3}$	50	$S_{1:3}$
4	100	$S_{0:2}$	30	$S_{0:2}$
4A	100	$S_{1:3}$	30	$S_{1:3}$
5	100	$S_{0:2}$	30	$S_{0:2}$
5A	100	$S_{1:3}$	30	$S_{1:3}$

Research Center near Nashua. The soil type was Readlyn loam (fine-loamy, mixed, mesic Aquic Hapludoll) at Nashua. Prior to planting, the experimental areas received broadcast applications of N, P, and K at rates of 34-22-28 and 45-0-0 kg ha^{-1} at Ames and Nashua, respectively. Sowing dates were

5 April at Ames and 13 April at Nashua. A plot was a hill sown with 20 seeds, and hills were spaced 30 cm apart in perpendicular directions. Two rows of hills were sown around each replication to provide competition for peripheral plots. Plots at Nashua were sprayed with a systemic fungicide to control fungal foliar diseases.

Traits measured or calculated were as follows. Recorded on a plot basis at Ames only: heading date (HD) as the number of days from planting until 50% of panicle emerged; and plant height (HT) as the distance (cm) from ground to tips of panicles. Recorded on a plot basis at all sites: biomass (BM) i.e., dry weight of bundle of culms in Mg ha^{-1}; grain yield (GY) i.e., the dry weight of threshed grain in Mg ha^{-1}; and harvest index (HI) calculated as (GY/BM) x 100%. Seed lots from the two replications of an entry at a site were combined, and the following traits were measured on the seed bulks: seed weight (SW) of 100 seeds in g; test weight (TW) measured by using a 78 ml container in kg m^{-3}; groat fraction (GF); the ratio of groat to seed weight measured on a 10 to 12 g sample dehulled mechanically in g kg^{-1}; groat yield (GTY) calculated as (GY x GF)/1000 in Mg ha^{-1}; groat-oil content (GO) measured on 4 to 6 g of groats by NMR spectroscopy in g kg^{-1}; and groat-oil yield (OY) calculated as (GTY x GO)/1000 in Mg ha^{-1}.

Statistical Analyses

Data for GO of the random lines were subjected to an analysis of variance. Locations and genotypes were considered random effects and cycles fixed. Within each regime, Satterthwaite's approximate F-test procedure was used to test for cycle main effects, and Fisher's protected L.S.D.-test was used to compare cycle means. The genotype-location interaction mean square for each cycle of selection was tested for significance against the error mean square obtained from the analysis of the checks. For each cycle of selection, variance components due to genotypes (σ^2_G) were estimated as linear functions of the appropriate mean squares. Approximate confidence intervals for $\hat{\sigma}^2_G$ were calculated by using the method of Bulmer (1957). Estimates of broad-sense heritability (H^2) were computed on an entry mean basis for each cycle in each regime. Exact 90% confidence intervals for H^2 were calculated by applying the method of Knapp et al. (1985).

Orthogonal polynomial regressions of GO on cycles of selection were computed for each regime to partition the variation due to cycles into variation due to linear effects, quadratic effects, and deviations from regression. A linear orthogonal regression was calculated for regime 2. Significance of linear (β_l) and quadratic (β_q) regression coefficients was determined by testing the mean square of the

linear and quadratic effects against the location-cycle interaction mean square. Next, the polynomial regression of GO on years was computed such that the linear regression coefficient (β_1') represented the response in GO on an annual basis. Slopes were tested for homogeneity (Snedecor and Cochran, 1980) to determine which recurrent selection regime was the most effective for increasing GO.

Data for GO of the selected lines of each regime were also subjected to analyses of variance. Genotypes and cycles were considered fixed effects and locations random. Within each regime, Fisher's protected L.S.D.-test was used to compare cycle means.

Finally, analyses of variance were computed utilizing data of all traits from the 10 oat lines with the greatest OY. Genotypes were considered fixed effects and Fisher's protected L.S.D.-test was used to compare means.

RESULTS AND DISCUSSION

Cycle effects were significant in regimes 1 and 3 but not in regime 2 (analyses of variance not shown) for both random and selected lines (Table 2). The genotype-location interaction was significant for each cycle of selection in each regime, but the interaction mean squares were small. This latter result agrees with earlier reports by Thro and Frey (1984), Gullord (1986), and Branson and Frey (1989). In regime 1, GO increased from 91.66 g kg^{-1} in the C_0 to 131.15 g kg^{-1} in the C_6, which is a 7.2% increase per year. An annual increase of 5.0% was accomplished in regime 2. After 2.5 cycles of selection of regime 3, GO increased from 112.16 g kg^{-1} to 142.08 g kg^{-1}, which is equivalent to a 10.7% improvement per year. Selection among S_0 plants in the field and among and within $S_{0:1}$ progenies in the greenhouse both contributed to the increase in GO in regime 3 (Fig. 2). The average GO of the 16 original parents was 77.65±2.08 g kg^{-1}, and that of the checks was 69.16±3.06 g kg^{-1}.

Linear regressions ($\hat{\beta}_1$) for GO on cycles of selection were 6.04, 3.97, and 6.02 g kg^{-1} for regimes 1, 2, and 3, respectively (Table 3). Quadratic regressions ($\hat{\beta}_q$) were not significant for regimes 1 and 3 and variation due to linear effects was not significant in regime 2 (analyses of variance not shown). Regression of GO on an annual basis was 6.04 for regime 1, 5.85 for regime 2, and 11.98 g kg^{-1} for regime 3.

Figure 2. Response of groat-oil content to three recurrent selection regimes

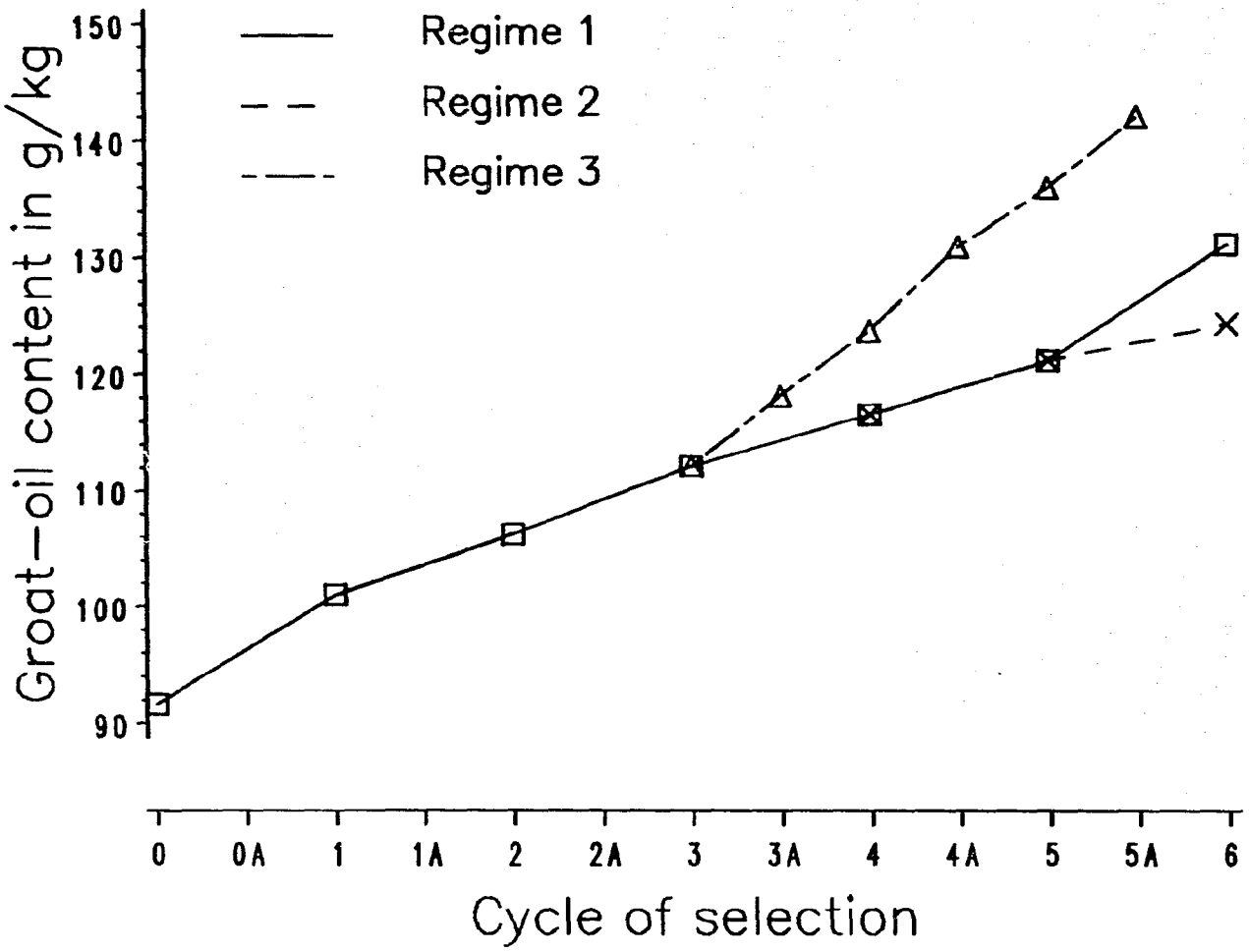

Regime 1
Regime 2
Regime 3
Groat–oil content in g/kg
150
140
130
120
110
100
90
0
0A
1
1A
2
2A
3
3A
4
4A
5
5A
6
Cycle of selection

Table 2. Means of G0 for random and selected lines of each cycle of selection and realized heritabilities for regimes 1, 2, and 3

Cycle	Random lines	Selected lines
	— g kg^{-1} —	— g kg^{-1} —
	Regime 1	
0	91.66±0.99[a]	98.76±1.34
1	101.02±0.92	106.06±1.23
2	106.25±0.83	111.52±1.23
3	112.16±0.85	117.45±1.29
4	116.58±1.12	123.76±1.99
5	121.18±0.99	131.54±1.76
6	131.15±0.98	-
$FLSD_{0.05}$	2.54	4.79
	Regime 2	
4	116.58±1.12	123.76±1.99
5	121.19±1.16	126.10±1.67
6	124.32±0.95	-
$FLSD_{0.05}$	ns	ns
	Regime 3	
3	112.16±0.85	117.45±1.29
3A	118.21±1.11	124.95±1.66
4	123.75±0.92	130.83±1.66
4A	130.91±1.00	136.21±1.66
5	136.00±0.81	141.63±1.49
5A	142.08±0.95	144.68±1.96
$FLSD_{0.05}$	4.01	3.90

[a]90% confidence interval

The test of homogeneity of the annual gains in G0 for regimes 1 and 2 was not significant ($\alpha>0.05$). The annual gain in G0 for regime 3 was significantly larger than those of regimes 1 and 2. Because more cycles of selection can be conducted in

Table 3. Polynomial regressions of GO on cycles of selection and annual response in GO for regimes 1, 2, and 3

Regime	Polynomial regression			Annual response
	Mean	$\hat{\beta}_1$	$\hat{\beta}_q$	$\hat{\beta}_1$
	g kg^{-1}			g kg^{-1}
1	111.58	6.04**	-0.04	6.04 a[a]
2	121.19	3.97		5.85 a
3	127.30	6.02**	-0.02	11.98 b

[a]Different letters indicate test of homogeneity was significant at the 0.01 probability level.
**Significant at the 0.01 probability level.

a year for regime 2, the number of hours involved in conducting it is greater than that for regime 1 on an annual basis. Further, because regime 2 is conducted only in the greenhouse, there can be no visual selection for agronomic traits as is done in the field. Thus, for these reasons, regime 2 is not a viable recurrent selection procedure for oat. Regime 3, with additional selection among S_1 plants within selected $S_{0:1}$ lines in the greenhouse, was very effective for obtaining greater increase in GO. The extra generation of selection in the greenhouse nearly doubled the annual gain from regime 1. The results are in agreement with predicted genetic gains in GO reported by Schipper (1991). Branson and Frey (1989), who evaluated the first three cycles of selection of regime 1, obtained an increase of 9.26 g kg^{-1} in GO, whereas in this study a linear increase of 6.04 g kg^{-1}

was obtained during six cycles of selection. This differential may be caused partly because the means for random lines in the C_0 and C_1 were higher than in the study of Branson and Frey (1989).

Five cycles of selection in regime 1 did not change $\hat{\sigma}^2_G$ for GO significantly (Table 4), but the $\hat{\sigma}^2_G$ of C_6 was significantly smaller than that of C_4 and C_5. Similarly, regime 3 had $\hat{\sigma}^2_G$'s in C_5 and C_{5A} that were smaller than in earlier cycles. Genetic variances in the last cycle of selection for each regime showed downward trends. Whether this represents an artifact of sampling, genetic drift, or real reductions cannot be discerned from this study. However, in no instance, did the confidence intervals for $\hat{\sigma}^2_G$ include the value zero. Thus, further progress of selection for GO can be expected. Genetic variances were larger in cycles C_{3A}, C_{4A}, and C_{5A} than in cycles C_3, C_4, and C_5, respectively, a result expected because $\hat{\sigma}^2_G$'s in C_{3A}, C_{4A}, and C_{5A} represent genetic variability among S_1 plants, whereas $\hat{\sigma}^2_G$ in C_3, C_4, and C_5 represents genetic variability among S_0 plants.

Except for the C_6 of regime 1 and C_5 and C_{5A} of regime 3, all H^2's are similar to previously reported heritabilities (Baker and McKenzie, 1972; Brown et al., 1974; Branson and Frey, 1989). The smallest H^2 was 0.50 in the C_6 of regime 1. Absence of consistent changes in H^2 in all regimes indicated that selection for GO did not influence the H^2 for this

Table 4. Genetic variances ($\hat{\sigma}^2_G$) and broad-sense heritabilities (H^2) for GO for each cycle of selection in regimes 1, 2, and 3

Cycle	$\hat{\sigma}^2_G$		H^2	
		Regime 1		
0	34.59	23.52-49.59[a]	0.67	0.54-0.76
1	35.47	25.34-49.51	0.73	0.62-0.81
2	30.39	22.07-41.99	0.75	0.66-0.82
3	33.98	25.24-45.99	0.76	0.68-0.83
4	55.03	39.85-75.79	0.73	0.63-0.80
5	46.85	34.83-63.51	0.77	0.69-0.84
6	21.43	11.33-34.13	0.50	0.31-0.64
		Regime 2		
4	55.03	39.85-76.79	0.73	0.63-0.80
5	58.06	41.26-80.85	0.70	0.59-0.79
6	45.18	34.29-60.69	0.83	0.69-0.84
		Regime 3		
3	33.98	25.24-45.99	0.76	0.68-0.83
3A	64.62	38.89-75.87	0.70	0.59-0.78
4	48.85	37.47-64.75	0.83	0.76-0.87
4A	61.68	48.14-80.81	0.87	0.83-0.91
5	19.86	11.94-29.91	0.55	0.38-0.67
5A	27.66	17.19-41.18	0.58	0.42-0.69

[a]90% confidence interval.

trait. From 50 to 87% of the variance for GO in the populations was genetic.

A goal of recurrent selection is the development of a population with a high frequency of superior lines. Frequency distributions (Table 5) show that recurrent selection for GO increased not only the means but also the

Table 5. Frequency distributions for GO of oat lines from each cycle of selection of regimes 1, 2, and 3

Class of GO	Cycle															
	Regime 1							Regime 2			Regime 3					
	0	1	2	3	4	5	6	4	5	6	3	3A	4	4A	5	5A
— g kg^{-1} —	%							%			%					
55.0- 64.9					1			1								
65.0- 74.9																
75.0- 84.9	18	1														
85.0- 94.9	55	18	3	1					2		1	1				
95.0-104.9	24	54	41	11	4	1		4			11	4		1		
105.0-114.9	3	23	47	51	35	19		35	23	12	51	31	13	2		
115.0-124.9		4	9	35	47	48	18	47	39	40	35	44	42	19	4	
125.0-134.9				2	12	26	55	12	30	40	2	17	37	45	36	18
135.0-144.9					1	6	25	1	6	8		2	8	28	56	49
145.0-154.9							2					1		5	4	31
155.0-164.9																2

groat-oil contents of the highest lines. Frequency distributions of C_0 and C_6 in regime 1 did not overlap; i.e., the groat-oil contents of all lines in the C_6 were higher than that of any line in the C_0. In regime 3, only one line in C_3 exceeded the line with the lowest GO in the C_{5A}. Frequency distributions changed only slighty over cycles for regime 2, which is further evidence that this regime was less effective than regimes 1 and 3 for increasing GO of oat.

Line M022-4-5 (regime 3, C_{5A}) with an average GO of 162.85 g kg^{-1} had the largest GO in the evaluation experiment. Frey and Hammond (1975) estimated that groat-oil contents of 160 g kg^{-1} are needed for economical extraction of oil from oat. Thus, line M022-4-5 would be a potential candidate for use in oat oil production.

To be useful in breeding programs, a line with a high GO also must produce a high GY and have favorable agronomic trait expressions. Mean values for 11 traits for the 10 oat lines with the highest OY are presented in Table 6. Five high-OY lines had GYs significantly higher than the mean of the checks. The HD, HT, HI, GTY, and GF values for these lines were similar to those of the checks. However, seven of the lines had significantly lower values for TW. All high-OY lines had significantly lower SW's than did the checks. In general, however, the 10 high-OY lines would be good parents for breeding programs.

Table 6. Means for 11 traits of 10 oat lines ranked highest for OY and of checks

Line	Regime	Cycle	Trait										
			OY	GO	BM	GY	GTY	HD	HT	HI	GF	SW	TW
			Mg ha^{-1}	g kg^{-1}	Mg ha^{-1}			d	cm	%	g kg^{-1}	g	kg m^{-3}
M020-8	3	5	0.483	138.7	11.06	5.25	3.48	66	89	47.6	661	2.52	411.2
L994-8	3	5	0.474	140.0	10.71	5.19	3.38	68	89	48.5	652	2.37	366.4
L343-3-5	3	4A	0.445	149.6	9.96	4.50	2.99	68	87	45.2	664	1.88	367.2
L228-1-5	3	4A	0.440	139.2	10.33	4.84	3.16	68	91	46.8	654	2.07	374.9
L343-3-2	3	4A	0.438	136.7	10.47	4.68	3.21	67	82	44.9	686	2.10	389.4
L343-3	3	4	0.436	140.7	9.98	4.71	3.10	68	89	47.4	659	1.94	377.6
N076	1	6	0.434	136.8	9.10	4.27	3.16	65	99	47.2	744	2.41	392.7
M043-7	3	5	0.431	142.7	9.10	4.52	3.02	65	86	50.8	668	2.29	430.1
M002-7	3	5	0.430	137.1	10.04	4.72	3.14	64	87	47.1	664	2.20	413.1
M042-17	3	5	0.430	153.9	9.39	4.30	2.80	70	83	45.8	650	2.04	380.3
$FLSD_{0.05}$			ns	ns	1.35	0.64	ns	3	ns	ns	ns	0.21	ns
Checks			0.196	69.2	9.07	4.28	2.84	67	91	47.5	662	2.84	422.5
$FLSD_{0.05}$[a]			0.058	10.2	1.00	0.41	ns	2	7	ns	ns	0.21	28.3

[a]Applicable for comparison of checks with oat lines high in OY.

In summary, this study showed that GO of oat increased linearly and significantly in recurrent selection regimes 1 and 3. Regime 3, which utilized an extra generation of selection in the greenhouse, was the most effective in increasing GO. Selection among S_0 plants in the field and selection among and within $S_{0:1}$ lines in the greenhouse both contributed to the increase in GO. Regime 2 was not viable for maximizing gain in GO. Selection in regimes 1 and 3 did not exhaust genetic variability for GO, so continued increase in GO can be expected.

REFERENCES

Baker, R.J., and R.I.H. McKenzie. 1972. Heritability of oil content in oats, Avena sativa L. Crop Sci. 12:201-202.

Branson, C.V., and K.J. Frey. 1989. Recurrent selection for groat oil content in oat. Crop Sci. 29:1382-1387.

Brown, C.M., A.N. Aryeetey, and S.N. Dubey. 1974. Inheritance and combining ability for oil content in oats (Avena sativa L.). Crop Sci. 14:67-69.

Bulmer, M.G. 1957. Approximate confidence limits for components of variance. Biometrika 44:159-167.

Burton, J.W., and C.A. Brim. 1981. Recurrent selection in soybeans. III. Selection for increased percent oil in seeds. Crop Sci. 21:31-34.

Conway, T.F., and F.R. Earle. 1963. Nuclear magnetic resonance for determining oil content of seeds. J. Am. Oil Chem. Soc. 40:265-268.

Frey, K.J. 1965. The utility of hill plots in oat research. Euphytica 14:196-208.

Frey, K.J., and E.G. Hammond. 1975. Genetics, characteristics, and utilization of oil in caryopses of oat species. J. Am. Oil Chem. Soc. 52:358-362.

Frey, K.J., E.G. Hammond, and P.K. Lawrence. 1975. Inheritance of oil percentage in interspecific crosses of hexaploid oats. Crop Sci. 15:94-95.

Frey, K.J., J.K. McFerson, and C.V. Branson. 1988. A procedure for one cycle of recurrent selection per year with spring-sown small grains. Crop Sci. 28:855-856.

Gullord, M. 1986. Oil and protein content in oats (Avena sativa L.). p. 210-213. In D.A. Lawes and H. Thomas (ed.) Proc. 2nd Int. Oats Conf. Aberystwyth, Wales. 15-18 July 1985. Martinus Nijhoff Publishers, Dordrecht, The Netherlands.

Hallauer, A.R. 1985. Compendium of recurrent selection methods and their application. CRC Crit. Rev. Plant Sci. 3:1-33.

Kalbasi-Ashtari, A. and E.G. Hammond. 1977. Oat oil: refining and stability. J. Am. Oil Chem. Soc. 54: 305-307.

Klein, S.J. 1990. Recurrent selection for test weight in oat. MS thesis. Iowa State Univ., Ames, IA.

Knapp, S.J., W.W. Stroup, and W.M. Ross. 1985. Exact confidence intervals for heritability on a progeny mean basis. Crop Sci. 25:192-194.

McDaniel, M.E., H.B. Kim, and B.R. Hattcock. 1967. Approach crossing of oats (Avena spp.). Crop Sci. 7:538-540.

McFerson, J.K. and K.J. Frey. 1990. Three selection strategies to increase protein yield in oats. J. Genet. Breed. 44:39-48.

Price, P.B., and J.G. Parsons. 1975. Lipids of seven cereal grains. J. Am. Oil Chem. Soc. 52:490-493.

Schipper, H. 1991. Section I. Selection for groat-oil content in oat grown in field and greenhouse. In H. Schipper. Comparison of three recurrent selection regimes for increasing groat-oil content of oat. Ph.D. dissertation. Iowa State Univ., Ames, IA.

Snedecor, G.W., and W.G. Cochran. 1980. Statistical methods. 7th ed. Iowa State Univ. Press, Ames, IA.

Thro, A.M., and K.J. Frey. 1984. Relationship between groat-oil content and grain yield of oats. (Avena sativa L.). Proc. Iowa Acad. Sci. 91:85-86.

Thro, A.M., and K.J. Frey. 1985. Inheritance of groat-oil content and high-oil selection in oats (Avena sativa L.). Euphytica 34:251-263.

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SECTION III.

RESPONSES IN AGRONOMIC TRAITS ASSOCIATED WITH THREE RECURRENT SELECTION REGIMES FOR GROAT-OIL CONTENT IN OAT

ABSTRACT

Crop strains with high values for the selected trait but unacceptable agronomic characteristics are not useful as varieties. In this study, it was determined whether selection for groat-oil content in oat (Avena sativa L.) via three recurrent selection regimes caused associated changes in 10 agronomic traits. Random lines of each cycle of selection of each regime were evaluated in a replicated field experiment at two locations. Biomass, grain yield, groat yield, and test weight decreased in all three regimes. Seed weight and plant height decreased in two regimes, and groat fraction in one. Oil yield increased in two regimes and decreased in the other. Plants headed earlier in one and later in another regime over cycles of selection. No changes in harvest index occurred. Heritabilities and genetic variances were relatively high for all traits in each regime. Factor analysis of the phenotypic correlation matrices indicated that simultaneous increases in grain yield and in groat-oil content are possible, that continuous selection for groat-oil content reduces groat fraction and test weight, and that seed weight is strongly and negatively associated with groat-oil content. A new recurrent selection regime for increasing groat-oil content of oat that may overcome the negative responses of agronomic traits was proposed.

INTRODUCTION

Recurrent selection for oil content in groats (caryopses) of oat has produced lines with groat-oil contents as high as 163 g kg^{-1} (Schipper, 1991b). Grain from oat lines with high groat-oil contents can be used as a high-caloric feed and as a source of culinary oil. One goal of recurrent selection is to develop a plant population both with a high frequency of lines superior for the trait under selection and with acceptable agronomic characteristics. Such lines can be good parents in breeding programs or candidates for release as cultivars.

Positive or negative associations between traits can cause correlated responses in recurrent selection programs. For example, three cycles of recurrent selection for high seed-oil content in soybean [*Glycine max* (L.) Merr.] caused decreasing trends in seed weight and in seed protein content (Burton and Brim, 1981). Seven cycles of within-HS family selection for oil content in maize (*Zea mays* L.) caused reductions in both kernel weight and ear height and increases in grain moisture (Miller et al., 1981). Misevic and Alexander (1989) reported decreases in grain yield, plant height, ear height, 500-kernel weight, ear length, and lodging, in addition to increases in grain moisture and ear row number, after 24 cycles of phenotypic recurrent selection for oil content of maize.

Factor analysis is a statistical procedure that groups traits that are associated with each other but not with traits in other groups. Factor analysis was used to determine the relations among traits related to yield by Walton (1971) in wheat (Triticum aestivum L.), by Denis and Adams (1978) in dry bean (Phaseolus vulgaris L.), and by Rattunde et al. (1989) in pearl millet (Pennisetum glaucum L.). Factor analysis can also be used to study the structure of correlation matrices of selected and unselected traits over cycles of recurrent selection.

In this study, the objectives were to determine whether selection for groat-oil content in oat via three recurrent selection regimes caused (1) changes in unselected agronomic traits, (2) changes in genetic variance and in heritability of unselected traits, (3) changes in the genetic correlations of groat-oil content with unselected traits, and (4) changes in the structure of the phenotypic correlation matrix of groat-oil content and unselected traits.

MATERIALS AND METHODS

Genepool Development and Selection Procedures

To develop the base population (C_0) for this study, eight high-oil A. sativa cultivars were crossed to eight high-oil A. sterilis accessions. To obtain three-way matings the single crosses were mated to eight A. sativa cultivars with good agronomic traits. Selection was practiced among S_1 plants for appropriate seed traits, maturity, plant height, and high groat-oil content, after which selected S_1-derived lines were intercrossed. After two cycles, agronomically acceptable lines with high groat-oil content were crossed randomly to five A. sativa cultivars. Intermating among the S_0 plants provided the seed for the C_0. The development of the gene pool is described in detail by Branson and Frey (1989a).

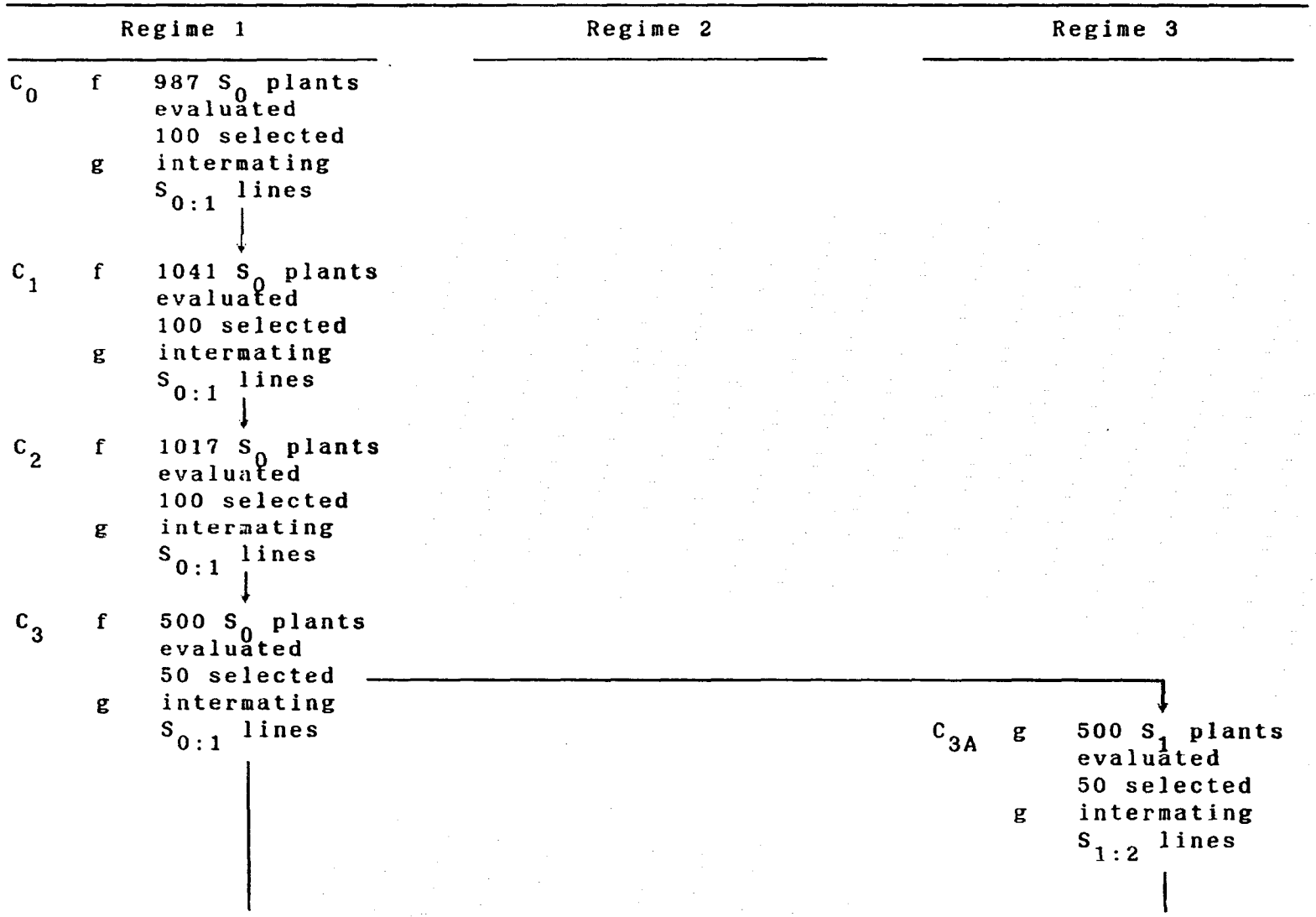
Recurrent selection regime 1 was initiated in 1983. Approximately 3500 S_0 seeds of the C_0 were space-sown in rows in the field. A row was 3 m long and contained a FS family of plants. Rows were spaced 90 cm apart. The plants were grown at the Agronomy and Agricultural Engineering Field Research Center near Ames, Iowa, on a Nicollet silty loam (fine-loamy, mixed, mesic Aquic Hapludoll). Before planting, the experimental area received a broadcast application of 34, 22, and 28 kg ha^{-1} of N, P, and K, respectively. At emergence and at weekly intervals thereafter, plants were

sprayed with an insecticide to kill aphids transmitting the barley yellow dwarf virus.

Visual selection was practiced among S_0 plants for desired height and maturity, panicle type, and seed shape and color. About 1000 S_0 plants were harvested, and a sample of seeds was dehulled from each to provide 3.5 to 6.0 g of groats for groat-oil analysis by wide-line nuclear magnetic resonance (NMR) spectroscopy (Conway and Earle, 1963). The 100 S_0 plants with the greatest groat-oil contents were selected, except that no more than one plant was selected from any FS family. During winter the selected $S_{0:1}$ lines were intermated in the greenhouse with each line crossed to four others. The approximately 10 S_0 seeds per cross provided the materials for the first cycle of selection (C_1).

One year was required to complete a cycle of regime 1. The procedure was repeated six times (Fig. 1), except that (1) 500 S_0 plants were evaluated for groat-oil content in C_3, from which 50 were selected and each mated to three others; and (2) About 400 S_0 plants were analyzed for oil in C_4, C_5, and C_6, and 30 $S_{0:1}$ lines were selected and intermated.

Regime 2, initiated in 1987, was identical to regime 1 except that evaluation, selection, and intermating all were done in the greenhouse. The 30 selected S_0 plants from C_4 of regime 1 were intermated and the S_0 seeds sown in the greenhouse. Three S_0 plants were grown per pot in a mixture of peat, loam (Iowa soil), and sand in a 4:4:2 ratio. Perlite


Regime 1
Regime 2
Regime 3
C0 f 987 S0 plants evaluated 100 selected g intermating S0:1 lines
C1 f 1041 S0 plants evaluated 100 selected g intermating S0:1 lines
C2 f 1017 S0 plants evaluated 100 selected g intermating S0:1 lines
C3 f 500 S0 plants evaluated 50 selected g intermating S0:1 lines
C3A g 500 S1 plants evaluated 50 selected g intermating S1:2 lines

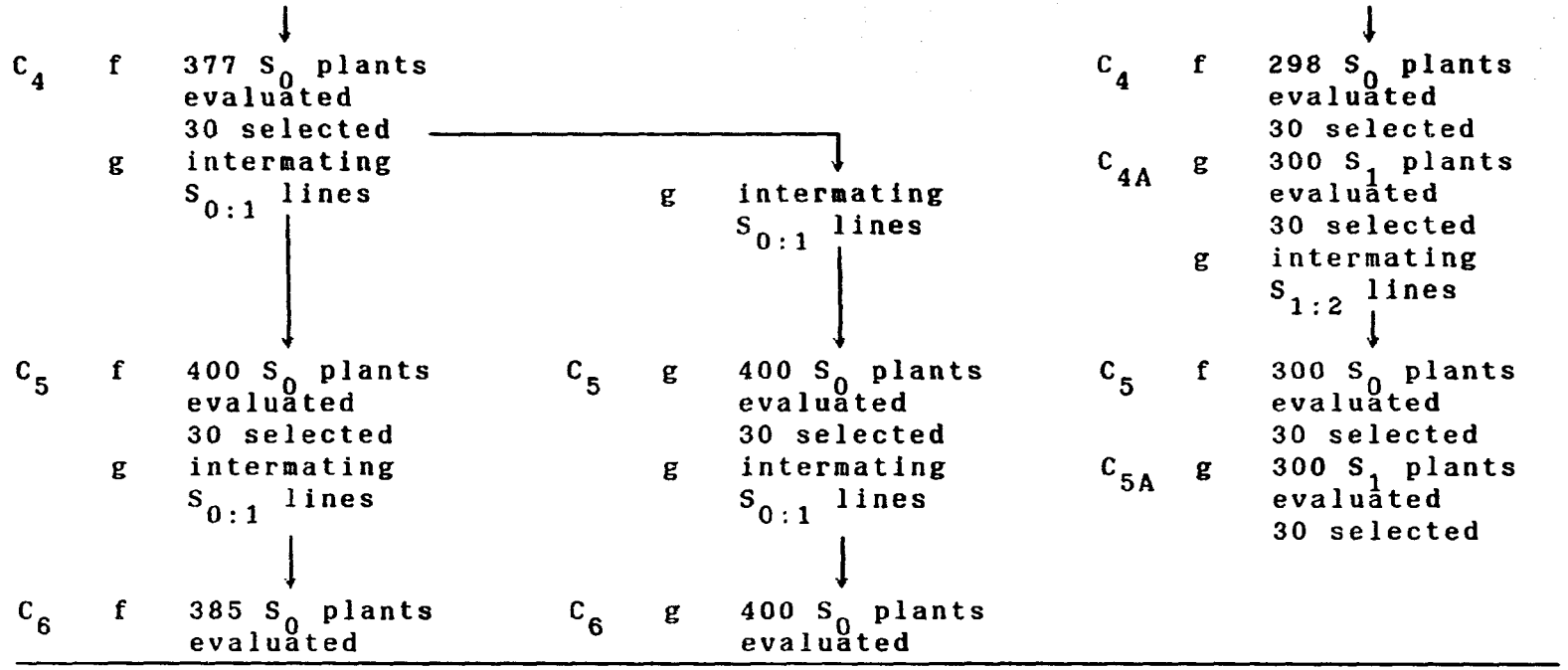


Figure 1. Flow chart of recurrent selection regimes 1, 2, and 3 (f or g indicate field- and greenhouse-grown, respectively)

was added to aid aeration. Pots were watered as needed, and a solution with N, P, and K was applied weekly. Plants were sprayed with insecticides and fungicides as needed. Temperature and day-length regimes were 21°C day/18°C night and 9 h, respectively, for a 5 wk period post-emergence and then 23°C day/18°C night and 15 h, respectively, until maturity. Thirteen-seed samples from 400 S_0 plants were dehulled and analyzed for groat-oil content, after which 30 $S_{0:1}$ lines were selected and intermated to form the C_5 population. This regime allowed for 1.5 cycles of recurrent selection per year and 2 cycles have been completed (Fig. 1).

Regime 3, initiated in September 1986, consisted of sowing in the greenhouse, 10 S_1 seeds from each of the 50 selected S_0 plants of the C_3 of regime 1. This population, which had 500 S_1 plants, was called C_{3A} (Fig. 1). Two plants were grown per pot, and pots were randomized on the bench. The environmental conditions were similar to those described for regime 2. At maturity the S_1 plants were harvested individually, and 13-seed samples were dehulled and analyzed for groat-oil content. Mean groat-oil content was computed for the 10 S_1 plants from each $S_{0:1}$ line, and the 80% $S_{0:1}$ lines with the highest mean groat-oil contents were selected. Next, 50 S_1 plants with highest individual groat-oil contents were selected and intermated in the greenhouse from December to March. Each $S_{1:2}$ line was crossed to three others, and approximately 10 S_0 seeds were obtained per

cross. These S_0 seeds, which formed the C_4, were space-sown in the field as described for regime 1.

The procedure was repeated for the fourth and fifth cycles of selection, except that groat-oil evaluations were made on 300 S_0 plants, and 30 were selected (Fig. 1). Thus, C_{4A} and C_{5A} each consisted of 300 S_1 plants. One cycle of this regime, with two generations of selection per cycle, required one year to complete.

Evaluation Experiment

An experiment to evaluate the effect of recurrent selection for higher groat-oil content in oat on agronomic traits, was conducted in 1989. It contained 100 random lines from each cycle of selection of each regime (Table 1). All selected lines were also evaluated, but only half of the selected lines were included for C_0, C_1, and C_2 of regime 1. Sixteen of the 29 original parents (Y22-15-9, Pettis, Lang, D2263032, Dal, Stout, Wright, IL75-5743, Y341-41, Otee, Spear, Mo-06195, Orbit, Lodi, Nya-11, and Hazel) and four checks (Starter, Webster, Hamilton, and Ogle) were entered into the experiment twice each. Thus, 1900 entries were evaluated. The evaluation experiment was grown in a randomized complete-block design with two replications at each of two locations in Iowa: the Agronomy and Agricultural Engineering Field Research Center near Ames and the Northeast Research Center near Nashua. At Nashua the soil type was

Table 1. Numbers and stages of oat lines evaluated for regimes 1, 2, and 3

Cycle	Random		Selected	
	Lines	Stages	Lines	Stages
		Regime 1		
0	100	$S_{0:3}$	50	$S_{0:3}$
1	100	$S_{0:3}$	50	$S_{0:3}$
2	100	$S_{0:3}$	50	$S_{0:3}$
3	100	$S_{0:2}$	50	$S_{0:2}$
4	100	$S_{0:2}$	30	$S_{0:2}$
5	100	$S_{0:2}$	30	$S_{0:2}$
6	100	$S_{0:1}$		
		Regime 2		
5	100	$S_{0:2}$	30	$S_{0:2}$
6	100	$S_{0:1}$		
		Regime 3		
3A	100	$S_{1:3}$	50	$S_{1:3}$
4	100	$S_{0:2}$	30	$S_{0:2}$
4A	100	$S_{1:3}$	30	$S_{1:3}$
5	100	$S_{0:2}$	30	$S_{0:2}$
5A	100	$S_{1:3}$	30	$S_{1:3}$

Readlyn loam (fine-loamy, mixed, mesic Aquic Hapludoll). Prior to planting, the experimental areas received broadcast applications of N, P, and K at rates of 34-22-28 and 45-0-0 kg ha^{-1} at Ames and Nashua, respectively. Sowing dates were 5 April at Ames and 13 April at Nashua. A plot was a hill

sown with 20 seeds, and hills were spaced 30 cm apart in perpendicular directions. Two rows of hills were sown around each replication to provide competition for peripheral plots. Plots at Nashua were sprayed with a systemic fungicide to control fungal foliar diseases.

The following traits were measured or calculated. Recorded on a plot basis at Ames only: heading date (HD) as the number of days from planting until 50% panicle emergence; and plant height (HT) as the distance (cm) from ground to tips of panicles. Recorded on a plot basis at all sites were: biomass (BM) i.e., the dry weight of bundle of the culms in Mg ha^{-1}; grain yield (GY) i.e., the dry weight of threshed grain in Mg ha^{-1}; and harvest index (HI), which was calculated as (GY/BM) x 100%. Seed lots from the two replications of an entry at a site were combined, and the following traits were measured on the seed bulks: weight of 100 seeds (SW) in g; test weight (TW) measured using a 78 ml container in kg m^{-3}; groat fraction (GF), the ratio of groat to seed weight measured on a 10 to 12 g sample dehulled mechanically in g kg^{-1}; groat yield (GTY) calculated as (GY x GF)/1000 in Mg ha^{-1}; groat-oil content (GO) measured on 4 to 6 g of groats by NMR spectroscopy in g kg^{-1}; and groat-oil yield (OY) calculated as (GTY x GO)/1000 in Mg ha^{-1}.

Statistical Analyses

Data for each unselected trait measured on the random lines, parents, and checks were subjected to an analysis of variance. Cycles as well as lines within cycles, were considered random effects; locations, parents, and checks were considered fixed. Within each regime, Satterthwaite's approximate F-test procedure was used to test for cycle main effects, and Fisher's protected L.S.D.-test was used to compare cycle means and to compare cycle means with parent and check means. For each cycle of selection, variance components due to genotypes (σ^2_G) were estimated as linear functions of the appropriate mean squares. A genetic variance was considered significant when the mean square for genotypes was significant. Broad-sense heritabilities (H^2) for unselected traits were estimated on an entry mean basis for each cycle of selection in each regime.

To measure the correlated responses with selection for GO, orthogonal polynomial regressions of unselected traits on cycles of selection were computed for each regime to partition the variation due to cycles into variations due to linear effects, quadratic effects, and deviations from regression. A linear orthogonal regression was computed for regime 2. Significance of the linear (β_l) and quadratic (β_q) regression coefficients was measured by testing the mean squares for linear and quadratic effects against the mean

square for location-cycle interaction. If the linear regression alone was significant, response per cycle of selection was $\hat{\beta}_1$. If the quadratic regression was also significant, response per cycle was calculated as $(C_6-C_0)/6$ for regime 1 and as $(C_{5A}-C_3)/5$ for regime 3.

Genetic correlations (r_G) were computed for GO with all other traits. Heading date and HT were measured only at Ames, so covariance analyses of the means of these traits with the means of GO measured at Nashua were used to obtain these r_G's. T-tests with Bonferonni adjustments to control the overall p-level (Bailey, 1977) were calculated to judge the significance of correlations.

To describe changes in the covariance structure of all traits associated with selection for high GO, factor analyses were conducted using the principal component method (Johnson and Wichern, 1988). The spectral decomposition of the phenotypic correlation matrix was computed for each selection cycle in each regime.

RESULTS AND DISCUSSION

Minor but significant changes occurred for HD over cycles of selection in regimes 1 and 3 (Table 2). Responses were -0.2 and 0.4 d cycle^{-1}, respectively (Table 3). The HD means in all cycles of selection were similar to the HD mean of the checks but smaller than that of the parents. The HT mean did not change over selection cycles in regime 1, but in regimes 2 and 3 the reponses were -1.2 and -0.7 cm cycle^{-1}, respectively. Total reduction in regime 3 was ca. 5 cm. Several cycle means for HT were significantly smaller than the HT mean of checks or parents. In the Midwestern U.S.A., short and early culivars of oat are favored.

Grain yield is the most important trait in oat breeding. To be useful in breeding programs, oat lines must have high GYs. Parents, on average, yielded less than the checks (Table 2). This was expected because parents were chosen primarily for high GO. In regime 1 the responses for BM, GY, and GTY were -0.09, -0.03, and -0.03 Mg ha^{-1} cycle^{-1}, respectively (Table 3). In regime 2, the responses were -0.86, -0.37, and -0.24 Mg ha^{-1} cycle^{-1} and in regime 3 -0.26, -0.13, and -0.09 Mg ha^{-1} cycle^{-1}, respectively for BM, GY, and GTY. Thus, in subsequent regimes, BM, GY, and GTY showed significant reductions. The reductions were especially large in regime 2; i.e., the regime entirely carried out in the greenhouse. In every cycle of selection,

Table 2. Means for 10 traits measured upon random oat lines from cycles of selection within regimes 1, 2, and 3, and upon checks and parents

Cycle	Trait									
	HD	HT	BM	GY	GTY	OY	HI	GF	TW	SW
	d	cm	Mg ha^{-1}				%	g kg^{-1}	kg m^{-3}	g
Regime 1										
0	67.3	88.9	8.41	3.81	2.51	0.230	45.5	660	417	2.65
1	66.5	88.4	8.25	3.70	2.47	0.249	45.0	667	416	2.61
2	66.4	89.0	7.95	3.56	2.38	0.253	45.0	668	407	2.59
3	65.7	89.2	8.33	3.79	2.51	0.281	45.8	663	408	2.46
4	66.1	88.0	8.35	3.78	2.49	0.290	45.4	659	398	2.35
5	66.2	87.6	7.48	3.37	2.23	0.271	45.2	658	383	2.36
6	66.3	88.2	8.01	3.65	2.38	0.312	45.8	652	381	2.29
$FLSD_{0.05}$	0.6	ns	0.43	0.10	0.10	0.013	ns	ns	11	0.18
Regime 2										
4	66.1	88.0	8.35	3.78	2.49	0.290	45.4	659	398	2.35
5	66.1	88.0	7.31	3.32	2.17	0.264	45.4	656	382	2.36
6	65.9	85.7	6.68	3.05	1.97	0.246	45.7	654	380	2.26
$FLSD_{0.05}$	ns	1.6	0.41	0.19	0.12	0.015	ns	ns	14	ns

Table 2. (Continued)

Cycle	Trait									
	HD	HT	BM	GY	GTY	OY	HI	GF	TW	SW
	d	cm	Mg ha^{-1}				%	g kg^{-1}	kg m^{-3}	g
Regime 3										
3	65.7	89.2	8.33	3.79	2.51	0.281	45.8	663	408	2.46
3A	66.4	86.6	7.99	3.57	2.35	0.277	44.8	659	391	2.34
4	65.9	87.8	8.43	3.82	2.53	0.314	45.5	664	393	2.24
4A	65.9	84.9	8.14	3.66	2.42	0.317	45.0	659	393	2.20
5	66.3	87.1	7.80	3.53	2.34	0.318	45.4	662	385	2.17
5A	67.5	84.3	7.05	3.15	2.06	0.293	44.8	665	367	2.14
$FLSD_{0.05}$	0.7	1.5	0.61	0.19	0.13	0.014	ns	ns	13	0.12
Checks										
	66.8	90.5	9.07	4.28	2.84	0.196	47.5	662	422	2.84
$FLSD_{0.05}$[a]	1.3	3.4	0.67	0.28	0.23	0.030	1.3	13	13	0.12
Parents										
	69.0	90.4	8.84	3.94	2.59	0.201	44.8	656	426	2.66
$FLSD_{0.05}$[a]	0.7	1.9	0.38	0.16	0.12	0.016	0.7	7	7	0.07

[a]Applicable for comparison of cycle means with checks or parents mean.

Table 3. Polynomial regressions and response per cycle of selection (R) for 10 traits for recurrent selection regimes 1, 2, and 3

Trait	Regime 1			
	Mean	$\hat{\beta}_1$	$\hat{\beta}_q$	R
HD, d	66.0	-0.1**	0.1**	-0.2
HT, cm	88.6	-0.2	-0.0	-
BM, Mg ha^{-1}	8.13	-0.09**	-0.00	-0.09
GY, Mg ha^{-1}	3.67	-0.03**	0.00	-0.03
GTY, Mg ha^{-1}	2.44	-0.03**	-0.00	-0.03
OY, Mg ha^{-1}	0.272	0.012**	-0.001	0.012
HI, %	45.5	0.1	0.0	-
GF, g kg^{-1}	665	-2*	-1	-2
TW, kg m^{-3}	404	-7**	-1	-7
SW, g	2.47	-0.06**	0.00	-0.06

*,**Significant at the 0.05 and 0.01 probability levels, respectively.

Regime 2			Regime 3			
Mean	$\hat{\beta}_1$	R	Mean	$\hat{\beta}_1$	$\hat{\beta}_q$	R
66.1	-0.2	-	66.0	0.3**	0.1**	0.4
88.0	-1.2**	-1.2	86.5	-0.7**	0.1	-0.7
7.30	-0.86**	-0.86	8.22	-0.21**	-0.09**	-0.26
3.32	-0.37**	-0.37	3.71	-0.10**	-0.04**	-0.13
2.18	-0.24**	-0.24	2.46	-0.06**	-0.03**	-0.09
0.265	-0.019**	-0.019	0.314	0.006**	-0.004**	0.002
45.7	0.0	-	45.1	-0.1	0.0	-
656	-2	-	662	-1	-0	-
382	-10*	-10	392	-6**	-1	-6
2.36	-0.04	-	2.22	-0.06**	0.01	-0.06

means for GY were significantly lower than the check mean. Schipper (1991b), however, found several lines in regimes 1 and 3 that had high GO and higher GYs than the checks. To prevent further decreases in GY, changes in the selection procedures should be considered.

The OY increased significantly in regimes 1 and 3, but in regime 3 the response was small (0.002 Mg ha^{-1} $cycle^{-1}$). Oil yield decreased significantly in regime 2. No changes occured for HI in any regime. Generally, the cycle means for HI were between 1.7 and 2.7% smaller than was the check mean. Cycle means for GF did not differ in any regime (Table 2). But for regime 1 the response was -2 g kg^{-1} $cycle^{-1}$.

Test weight, an index of quality and influenced by both the density and packing efficiency of the grain, decreased significantly in all regimes. Responses were -7, -10, and -6 kg m^{-3} $cycle^{-1}$ in regimes 1, 2, and 3, respectively. Small values for TW are undesirable. Reductions in TW may have been caused by changes in shape of the groats. Selection for high GO clearly changed the groats from short and plump to long and slender. The response in SW was -0.06 g $cycle^{-1}$ in regimes 1 and 3 (Table 3). All cycle means for SW were significantly smaller than the mean of the checks. Seed germination has not been reduced to date, but the decrease of SW is of concern.

Branson and Frey (1989b) evaluated the first three cycles of selection in regime 1 and found no significant

change for any unselected trait. Miller et al. (1981) found that over seven cycles of selection for oil content in maize, kernel weight was reduced but that grain yield and plant height did not change. Misevic and Alexander (1989), however, found that 24 cycles of phenotypic recurrent selection for oil content caused a reduction in grain yield, plant height, and 500-kernel weight. Burton and Brim (1981) observed a decrease in seed weight but no changes in maturity or seed yield after three cycles of recurrent selection for seed-oil content of soybean. Thus, all studies including the present one, have shown a reduction in seed weight with selection for increased oil content.

The ∂_G^2 values for all traits generally were significant in all cycles of selection in all regimes (Table 4). For HD, HT, HI, and GF, the ∂_G^2 did not show change over cycles in regime 1. But the ∂_G^2 for BM, GY, GTY, and OY increased, and the ∂_G^2 for TW and SW decreased. Mean squares among genotypes for TW and SW, however, remained significant. The reduction in ∂_G^2 was 42% for TW and 57% for SW. Similar trends for ∂_G^2 of all traits were observed for regime 2. For regime 3, ∂_G^2's of all traits were markedly higher in C_{3A}, C_{4A}, and C_{5A} than in C_3, C_4, and C_5, respectively. This was caused by the fact that the genetic variance in C_3, C_4, and C_5 was among S_0-derived lines (Table 1) whereas the genetic variance in C_{3A}, C_{4A}, and C_{5A} was the sum of that among S_0-derived lines plus that among S_1-derived lines within

Table 4. Genetic variances ($\hat{\sigma}^2_G$) for 10 traits of oat within cycles of selection in regimes 1, 2, and 3 of recurrent selection

Cycle	Trait									
	HD	HT	BM	GY	GTY x10^4	OY x10^4	HI	GF	TW	SW x10^4
					Regime 1					
0	4.87**	28.6**	0.576**	0.109**	440**	4.45**	3.06*	233**	509**	482**
1	2.62**	14.2**	0.383**	0.088**	370**	5.45**	2.53**	260**	326**	338**
2	2.64**	27.5**	0.425**	0.081**	265*	3.27	2.34*	168**	428**	222**
3	3.45**	21.3**	0.631**	0.178**	796**	13.21**	2.32*	186**	214**	269**
4	2.37**	27.4**	0.618**	0.142**	530**	8.09**	4.52	291**	315**	407**
5	5.00**	35.6**	0.860**	0.246**	1140**	19.61**	4.33**	221**	377**	369**
6	3.61**	23.5**	0.827**	0.165**	861**	16.14**	3.87**	548**	295**	209**
					Regime 2					
4	2.37**	27.4**	0.618**	0.142**	530**	8.09**	4.52	291**	315**	407**
5	3.57**	29.5**	1.008**	0.236**	1088**	20.28**	4.76*	300**	331**	291**
6	3.72**	20.7**	1.735**	0.396**	1866**	33.13**	5.93**	423**	298**	312**
					Regime 3					
3	3.45**	21.3**	0.631**	0.178**	796**	13.21**	2.32*	186**	214**	269**
3A	10.91**	37.7**	1.377**	0.303**	1178**	15.63**	6.19**	425**	608**	435**
4	2.22**	16.6**	0.670**	0.151**	704**	14.59**	2.69**	109**	210**	176**
4A	3.60**	24.6**	1.079**	0.314**	1198**	29.05**	7.35**	288**	513**	415**
5	3.63**	16.7**	0.896**	0.271**	1168**	23.01**	3.42**	168**	433**	157**
5A	10.64**	31.5**	1.500**	0.370**	1230**	23.21**	5.99**	289**	768**	154**

*,**Mean square for genotypes significant at the 0.01 and 0.05 probability levels, respectively.

S_0 progenies. Trends in $\hat{\sigma}^2_G$ for all traits in regime 3 were similar to those of regime 1, except for TW. In regime 1 the $\hat{\sigma}^2_G$ for TW decreased, whereas in regime 3 it increased.

In regime 1 H^2's for HD and HT were high (Table 5). Those for BM, GY, GTY, and OY were also high and tended to increase over cycles of selection in each regime. Harvest index had, on average, the lowest H^2's; for GF, TW, and SW, they were moderately high. The H^2's indicate that any trait in these populations could be modified by selection. Branson and Frey (1989b) reported low and declining values for the heritability of groat fraction.

In regimes 1 and 3, r_G's of GO with BM, GY, and GTY were low and mostly nonsignificant (Table 6), but in regime 2, they were significant and positive. Small r_G values between GO and GY are desired because such values indicate that these traits are inherited independently and thus that simultaneous improvement of both traits may be possible. The reduction in mean GY over cycles of selection in each regime (Table 2) should, therefore, be reversible. Branson and Frey (1989b) also found independence between grain yield and groat-oil contents over the first three cycles of regime 1. In other studies (Forsberg et al., 1974, Gullord, 1980, Thro and Frey, 1984), significant positive correlations were reported between these traits.

The r_G between GO and OY was significant and positive in

Table 5. Broad-sense heritability estimates (H^2) for 10 traits of oat within cycles of selection of regimes 1, 2, and 3 of recurrent selection

Cycle	Trait									
	HD	HT	BM	GY	GTY	OY	HI	GF	TW	SW
					Regime 1					
0	0.85	0.75	0.60	0.52	0.46	0.44	0.33	0.59	0.81	0.80
1	0.73	0.58	0.51	0.53	0.46	0.50	0.46	0.54	0.70	0.69
2	0.69	0.76	0.45	0.39	0.29	0.28	0.37	0.60	0.83	0.39
3	0.74	0.65	0.57	0.70	0.70	0.71	0.32	0.65	0.69	0.71
4	0.70	0.72	0.65	0.58	0.53	0.49	0.82	0.68	0.73	0.82
5	0.80	0.74	0.58	0.66	0.63	0.62	0.51	0.57	0.83	0.74
6	0.80	0.70	0.71	0.67	0.69	0.65	0.60	0.57	0.75	0.62
					Regime 2					
4	0.70	0.72	0.65	0.58	0.53	0.49	0.82	0.68	0.73	0.82
5	0.79	0.76	0.65	0.66	0.67	0.68	0.36	0.77	0.77	0.71
6	0.75	0.63	0.75	0.75	0.77	0.78	0.58	0.78	0.73	0.77
					Regime 3					
3	0.74	0.65	0.57	0.70	0.70	0.71	0.32	0.65	0.69	0.71
3A	0.93	0.83	0.78	0.75	0.72	0.66	0.64	0.74	0.86	0.78
4	0.66	0.70	0.65	0.64	0.62	0.62	0.47	0.37	0.69	0.64
4A	0.81	0.75	0.69	0.75	0.70	0.87	0.70	0.72	0.88	0.83
5	0.70	0.60	0.62	0.69	0.67	0.67	0.48	0.48	0.82	0.66
5A	0.91	0.78	0.80	0.83	0.77	0.74	0.47	0.65	0.89	0.60

Table 6. Genetic correlations (r_G) for GO with 10 traits of oat within cycles of selection of regimes 1, 2, and 3 of recurrent selection

Cycle	Trait									
	HD	HT	BM	GY	GTY	OY	HI	GF	TW	SW
					Regime 1					
0	0.06	0.10	-0.09	-0.19	-0.27	0.44**	-0.22	-0.26	-0.27	-0.38**
1	-0.00	-0.05	-0.04	-0.06	-0.08	0.56**	-0.05	-0.04	-0.03	-0.37**
2	-0.10	-0.03	-0.29*	-0.21	-0.32*	0.43**	0.25	-0.26	-0.01	-0.77**
3	0.05	0.11	0.17	0.12	0.11	0.50**	-0.11	-0.04	-0.08	-0.24
4	-0.00	-0.11	-0.30*	-0.30*	-0.30*	0.47**	-0.07	0.03	-0.14	-0.34**
5	0.03	-0.01	0.21*	0.08	0.01	0.38**	-0.21*	-0.41**	-0.32**	-0.47**
6	0.06	-0.16	0.20	0.12	-0.01	0.26	-0.18	-0.41**	-0.42**	-0.08
					Regime 2					
4	-0.00	-0.11	-0.30*	-0.30*	-0.30*	0.47**	-0.07	0.03	-0.14	-0.34**
5	-0.07	-0.12	0.39**	0.38**	0.32**	0.59**	0.15	-0.27	-0.35**	-0.34**
6	-0.06	-0.09	0.34**	0.36**	0.27	0.51**	0.29*	-0.50**	-0.25	0.03
					Regime 3					
3	0.05	0.11	0.17	0.12	0.11	0.50**	-0.11	-0.04	-0.08	-0.24
3A	-0.02	-0.09	-0.10	-0.21	-0.31*	0.09	-0.27*	-0.52**	-0.35**	-0.17
4	-0.09	-0.09	0.12	0.09	0.09	0.54**	-0.06	0.04	-0.28*	-0.42**
4A	-0.07	-0.01	0.29*	0.30*	0.28*	0.58**	0.16	-0.14	-0.25	-0.27
5	-0.13	-0.00	0.10	0.17	0.04	0.27*	0.27*	-1.02**	-0.36**	-0.08
5A	0.03	-0.01	-0.19	-0.22	-0.30*	-0.09	-0.28*	-0.48**	-0.77**	-0.87**

*,**Significant at the joint probability levels of 0.01 and 0.05, respectively.

most cycles of selection. A high oil content in groats would provide a high caloric value for feed oat, but a high yield of oil per ha is important from the standpoint of profitability of oat production. Thus, a high positive correlation between GO and OY is desirable. Oil yield is a product of GO and GTY, and GTY is a product of GY and GF. This shows the value of maintaining high GYs in a recurrent selection program for high GO.

Genetic correlations of GO with HD, HT, and HI were low and nonsignificant in all cycles of all regimes. This agrees with correlations reported by Branson and Frey (1989b). The r_G's of GO with GF and TW generally were negative, and the intensity of these genetic associations tended to increase over cycles of selection. In most cycles of all regimes, the r_G between GO and SW was negative and highly significant. A negative association was also reported by Branson and Frey (1989b). Independence was reported by Brown et al. (1966), Baker and McKenzie (1972), and Gullord (1980), and a positive correlation for these two traits was reported by Forsberg et al. (1974).

For the factor analyses, factor loadings $\geq|0.50|$ are indicated with + or -, depending on the sign of the loading (Table 7). The first three factors accounted for 63 to 75% of the total variance in the various cycles of selection. The first factor, which accounted for 34 to 42% of the total variance, can be called a yield factor. Biomass, GY, GTY,

Table 7. Trait loadings for factors 1, 2, and 3 obtained by factor analysis of cycles of selection in regimes 1, 2, and 3 of recurrent selection

Cycle	Regime	Trait											Percent variance explained
		HD	HT	BM	GY	GTY	OY	HI	GF	TW	SW	GO	
						Factor 1							
0	1			+	+	+	+						34
1	1			+	+	+	+						35
2	1			+	+	+	+						35
3	1		+	+	+	+	+						39
4	1			+	+	+	+						35
5	1			+	+	+	+	+					39
6	1		+	+	+	+	+						38
4	2			+	+	+	+						35
5	2			+	+	+	+						39
6	2			+	+	+	+						40
3	3		+	+	+	+	+						39
3A	3		+	+	+	+	+						38
4	3		+	+	+	+	+						39
4A	3			+	+	+	+	+					42
5	3		+	+	+	+	+						40
5A	3			+	+	+	+						40
						Factor 2							
0	1	-							+	+			16
1	1	-							+	+			16
2	1								+	+	-		16
3	1	-						+	+	+			16
4	1	-							+	+			17
5	1	-							+	+	+	-	19
6	1	-						+	+	+		-	23
4	2	-							+	+			17
5	2	-							+	+			19
6	2	+							-	-		+	12
3	3	-						+	+	+			16
3A	3	-						+	+	+		-	20
4	3	-								+			16
4A	3	-						+	+	+			16
5	3	-							+	+		-	17
5A	3	-						+	+	+		-	23

Table 7. (Continued)

Cycle	Regime	Trait											Percent variance explained
		HD	HT	BM	GY	GTY	OY	HI	GF	TW	SW	GO	
						Factor 3							
0	1										+	-	14
1	1										+	-	13
2	1	-										-	14
3	1										-	+	13
4	1						+				-	+	14
5	1		+								+		11
6	1										+		10
4	2						+				+	-	14
5	2		+								+		11
6	2	-						+			+		12
3	3										-	+	13
3A	3		+								+		12
4	3										+	-	13
4A	3										+		13
5	3										+	-	11
5A	3										-	+	12

and OY had high loadings on this factor, whereas HT and HI occasionally had moderate loadings. The yield factor showed the dependence of GTY and OY on GY, i.e. variation in OY and GTY was closely associated with variation in GY. The second factor explained 16 to 23% of the total variance and generally had high loadings for HD, GF, and TW. Because TW and GF determine the quality of oat, factor 2 can be called a seed-quality factor. This factor showed a strong negative association between maturity and quality. In several cycles,

HI and GO seemed to have moderate loadings on factor 2, indicating, respectively, a positive and a negative association with quality traits. The third factor explained 10 to 14% of the total variance and had high loadings for SW and GO. The opposite loading signs of these two traits indicated their strong negative association. In cycles in which GO had a low loading on factor 3, either the fourth or fifth factor was highly loaded by GO.

The factor analyses indicate that selection for GO in all three regimes did not alter the structure of the phenotypic correlation matrix in any consistent manner. The analyses do indicate, however, that although continued selection for GO may have a deteriorating effect on GF, TW, and SW, decreases in GY can be offset by simultaneous selection for GO and GY. The results also show the usefulness of factor analysis as a tool in studying correlated responses in recurrent selection programs.

To overcome the negative effects on yield and quality traits caused by recurrent selection for GO, a change in procedure is recommended. During summer, 3000-4000 S_0 plants should be space-sown in the field and about 1000 evaluated for GO. One hundred lines highest in GO are selected. During the next winter, 10 S_1 seeds from each of the 100 selected S_0 plants would be grown in the greenhouse for seed increase. In the second summer, the 1000 $S_{0:2}$ lines would be evaluated in a replicated field experiment at two or more

locations, and utilizing hill plots. Groat-oil content and agronomic traits would be recorded, and a restricted selection index, maximizing the genetic gain of GO while holding the response of other agronomic traits to no change, would be used to select 100 $S_{0:2}$ lines. Finally, during the second winter, $S_{2:3}$ lines would be intermated. This regime would require two years per cycle. Selection for GO among and within $S_{0:1}$ lines in the greenhouse, as practiced with regime 3, would be replaced by selection among and within $S_{0:2}$ lines in the field. The genetic gain in GO from the second selection in the replicated field experiment should be greater than that from regime 3 because the former selection would be based upon large seed samples from field-grown plants, replicated plots, and $S_{0:2}$ lines (Schipper, 1991a). Use of a restricted selection index, however, will not maximize the genetic gain in GO. An additional advantage of the proposed regime is that it requires only two generations per year, one each in the field and greenhouse, a factor that may make it applicable in many breeding programs.

REFERENCES

Bailey, B.J.R. 1977. Tables of the Bonferonni t statistic. J. Am. Stat. Assoc. 72:469-478.

Baker, R.J., and R.I.H. McKenzie. 1972. Heritability of oil content in oats, Avena sativa L. Crop Sci. 12:201-202.

Branson, C.V., and K.J. Frey. 1989a. Recurrent selection for groat oil content in oat. Crop Sci. 29:1382-1387.

Branson, C.V., and K.J. Frey. 1989b. Correlated response to selection for groat-oil content in oats. Euphytica 43:21-28.

Brown, C.M., D.E. Alexander, and S.G. Carmer. 1966. Variation in oil content and its relation to other characters in oats (Avena sativa L.). Crop Sci. 6: 190-191.

Burton, J.W., and C.A. Brim. 1981. Recurrent selection in soybeans. III. Selection for increased percent oil in seeds. Crop Sci. 21:31-34.

Denis, J.C., and M.W. Adams. 1978. A factor analysis of plant variables related to yield in dry beans. I. Morphological traits. Crop Sci. 18:74-78.

Conway, T.F., and F.R. Earle. 1963. Nuclear magnetic resonance for determining oil content of seeds. J. Am. Oil Chem. Soc. 40:265-268.

Forsberg, R.A., V.L. Youngs, and H.L. Shands. 1974. Correlations among chemical and agronomic characteristics in certain oat cultivars and selections. Crop Sci. 14:221-224.

Gullord, M. 1980. Oil and protein content and its relation to other characters in oats (Avena sp.). Acta Agric. Scand. 30:216-218.

Johnson, R.A., and D.W. Wichern. 1988. Applied multivariate statistical analysis. 2nd ed. Prentice-Hall, Englewood Cliffs, NJ.

Miller, R.I., J.W. Dudley, and D.E. Alexander. 1981. High intensity selection for percent oil in corn. Crop Sci. 21:433-437.

Misevic, D., and D.E. Alexander. 1989. Twenty-four cycles of phenotypic recurrent selection for percent oil in maize. I. Per se and test-cross performance. Crop Sci. 29:320-324.

Rattunde, H.F., J.R. Witcombe, and K.J. Frey. 1989. Structure of variation among morphological and physiological traits in three pearl millet composites. Euphytica 43:233-244.

Schipper, H. 1991a. Section I. Selection for groat-oil content in oat grown in field and greenhouse. In H. Schipper. Comparison of three recurrent selection regimes for increasing groat-oil content of oat. Ph.D. dissertation. Iowa State Univ., Ames, IA.

Schipper, H. 1991b. Section II. Three recurrent selection regimes to increase groat-oil content of oat. In H. Schipper. Comparison of three recurrent selection regimes for increasing groat-oil content of oat. Ph.D. dissertation. Iowa State Univ., Ames, IA.

Thro, A.M., and K.J. Frey. 1984. Relationship between groat-oil content and grain yield of oats (Avena sativa L.). Proc. Iowa Acad. Sci. 91:85-86.

Walton, P.D. 1971. The use of factor analysis in determining characters for yield selection in wheat. Euphytica 20:416-421.

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SECTION IV.

CHANGES IN FATTY ACID COMPOSITION ASSOCIATED WITH RECURRENT SELECTION FOR GROAT-OIL CONTENT IN OAT

ABSTRACT

Groat-oil of oat (Avena sativa L.) is a well-balanced oil with respect to saturated, monounsaturated, and polyunsaturated fatty acid contents. In this study, the effect of six cycles of recurrent selection for high groat-oil content on the fatty acid composition of the groat-oil was determined. From each cycle of selection, 50 oat lines were grown in a replicated field experiment at two sites and were evaluated for groat-oil content and fatty acid composition. Contents of palmitate and linolenate decreased moderately over cycles of selection, whereas stearate content increased. A major increase occurred in the content of oleate and a major decrease in linoleate. Most of the modification of fatty acid composition took place within the saturated and unsaturated classes. The ratio of unsaturated to saturated fatty acids increased over cycles of selection. Significant genetic variation was present for each fatty acid indicating that selection for different desired fatty acid compositions in groat-oil of oat should be possible in this population.

INTRODUCTION

The dietary quality of vegetable oil is judged by its fatty acid composition with respect to saturated, monounsaturated, and polyunsaturated fatty acids. The desired fatty acid composition in oil depends on its nutritional utilization (Anonymous, 1990).

Monounsaturated fatty acids, and specifically oleate (18:1), lower the plasma cholesterol level, thereby reducing the risk of coronary heart disease (Grundy, 1987). Saturated fatty acids, such as palmitate (16:0) and stearate (18:0), elevate the cholesterol levels in plasma. Recently, however, Bonanome and Grundy (1988) demonstrated that 18:0 is as effective as 18:1 in lowering plasma cholesterol levels. Polyunsaturated fatty acids such as linoleate (18:2) and linolenate (18:3) are essential in mammalian diets because mammals cannot convert monounsaturated fatty acids into polyunsaturated ones (Lehninger, 1982). Linoleate is the major cholesterol-lowering fatty acid (Hegsted et al., 1965) but it also cures dermatitis, or inflamation of the skin (Guthrie, 1989). Both 18:2 and 18:3 promote growth (Guthrie, 1989). However, a high proportion of 18:3 in a vegetable oil makes the oil unstable because 18:3 oxidizes easily (deMan, 1990). The recommended fatty acid composition for the total dietary fat has about equal proportions of saturated, monounsaturated, and polyunsaturated fatty acids (Vles and

Gottenbos, 1989).

Youngs and Püskülcü (1976) found that the average fatty acid composition of oil in groats (caryopses) from 15 oat (A. sativa L.) strains was 6 g kg^{-1} myristate (14:0), 189 g kg^{-1} 16:0, 16 g kg^{-1} 18:0, 364 g kg^{-1} 18:1, 405 g kg^{-1} 18:2, and 19 g kg^{-1} 18:3. Groat-oil contents in current oat cultivars range from 40 to 60 g kg^{-1} which is too low for economical extraction. However, Schipper (1991) created an oat line with 163 g kg^{-1} groat-oil, by utilizing recurrent selection in an A. sativa gene pool with A. sterilis alleles for high groat-oil content introgressed in it. Of crucial importance, of course, is the extent to which high groat-oil content may affect the fatty acid composition of groat-oil.

De la Roche et al. (1977) analyzed nine strains of oat and found that with increasing oil content the proportions of 16:0 and 18:2 decreased and that of 18:1 increased. The ratio of saturated to unsaturated fatty acids was similar for all nine strains. Burton et al. (1983) found that selection for increased 18:1 content in soybean [Glycine max (L.) Merr.] oil caused no change in oil content. Selection for percent oil in Nebraska B and Nebraska Krug maize (Zea mays L.) populations, caused an increase in 18:1 and a decrease in 18:2 in the Nebraska B population, whereas the opposite occurred in Nebraska Krug (Pamin et al., 1986). After 24 cycles of phenotypic recurrent selection for percent oil in maize, 18:1 increased and 18:2 decreased 1.39 g kg^{-1} $cycle^{-1}$

(Misevic and Alexander, 1989).

The objectives were to determine: (1) whether recurrent selection for increased groat-oil content in oat caused changes in contents of 16:0, 18:0, 18:1, 18:2, and 18:3 in the groat-oil, (2) the magnitude of the genetic variance and heritability of each fatty acid, and (3) the associations between fatty acids and groat-oil content.

MATERIALS AND METHODS

Genepool Development and Selection Procedures

To develop the base population (C_0) for this study, eight high-oil A. sativa cultivars were crossed to eight high-oil A. sterilis accessions. These single crosses were then mated to eight A. sativa cultivars that had good agronomic traits to give three-way matings. Selection was practiced among S_1 plants for appropriate seed traits, early maturity, short plant height, and high groat-oil content, after which selected S_1-derived lines were intercrossed. After two cycles, agronomically acceptable lines with high groat-oil content were crossed randomly to five A. sativa cultivars. Intermating among the S_0 plants provided seed for the C_0. The development of the gene pool is described in detail by Branson and Frey (1989).

Recurrent selection was initiated in 1983. Ca. 3500 S_0 seeds of the C_0 were space sown in rows in the field. A row was 3 m long and contained a FS family. Rows were spaced 90 cm apart. The plants were grown at the Agronomy and Agricultural Engineering Field Research Center near Ames, Iowa, on a Nicollet silty loam (fine-loamy, mixed, mesic Aquic Hapludoll). Before planting the experimental area received a broadcast application of 34, 22, and 28 kg ha^{-1} of N, P, and K, respectively. At emergence and at weekly intervals thereafter, plants were sprayed with an insecticide

to kill aphids that transmit the barley yellow dwarf virus.

Visual selection was practiced among S_0 plants for desired height, maturity, and seed and panicle types. About 1000 S_0 plants were harvested and a sample of seeds was dehulled from each to provide 3.5 to 6.0 g of groats for groat-oil analysis by wide-line nuclear magnetic resonance (NMR) spectroscopy (Conway and Earle, 1963). The 100 S_0 plants highest in groat-oil content were selected, except that no more than one plant was chosen from any FS family. During winter the selected $S_{0:1}$ lines were intermated in the greenhouse with each line being crossed to four others. The ca. 10 S_0 seeds per cross provided the materials for the first cycle of selection (C_1).

One year was used to complete a cycle of selection. The procedure was repeated six times, except that (1) 500 S_0 plants were evaluated for groat-oil content in C_3 from which 50 were selected and each was intermated to three others, and (2) about 400 S_0 plants were evaluated for oil in the C_4, C_5, and C_6 and 30 $S_{0:1}$ lines were selected and intermated.

Evaluation Experiment

An experiment to evaluate the effect of recurrent selection for higher groat-oil content in oat on the fatty acid composition of groat-oil, was conducted in 1989. It contained 50 random lines from each of the six cycles of

selection. Further, 20 lines with high groat-oil content (HO-lines), 16 of the 29 original parents (Y22-15-9, Pettis, Lang, D2263032, Dal, Stout, Wright, IL75-5743, Y341-41, Otee, Spear, Mo-06195, Orbit, Lodi, Nya-11, and Hazel), and four checks (Starter, Webster, Hamilton, and Ogle) were also entered into the experiment.

The 390 entries were grown in a randomized complete-block design with two replications at each of two locations in Iowa: the Agronomy and Agricultural Engineering Field Research Center near Ames and the Northeast Research Center near Nashua. The soil type was Readlyn loam (fine-loamy, mixed, mesic Aquic Hapludoll) at Nashua. Prior to planting, the experimental areas received broadcast applications of N, P, and K at rates of 34-22-28 and 45-0-0 kg ha^{-1} at Ames and Nashua, respectively. Sowing dates were 5 April at Ames and 13 April at Nashua. A plot was a hill sown with 20 seeds and hills were spaced 30 cm apart in perpendicular directions. Two rows of hills were sown around each replication to provide competition for peripheral plots. Plots at Nashua were sprayed with a systemic fungicide to control fungal foliar diseases.

After threshing, seed lots from the two replications of an entry at a site were combined and a sample of the bulk was dehulled to obtain 4 to 6 g of groats. Each sample of groats was analyzed by NMR spectroscopy for groat-oil content (GO). GO was expressed in g kg^{-1}. Next the contents of 16:0, 18:0,

18:1, 18:2, and 18:3 in the groat-oil were determined. Samples of about 1 g of groats were crushed between two plates in a hydraulic press at 1500 to 3000 kg cm^{-1}. One plate had 40 grooves 40 mm long, 8 mm wide, and 1.6 mm deep that were filled each with a groat sample. The samples of crushed groats were transferred to test tubes and extracted with hexane for about 18 h. Then about 0.1 ml of the hexane was transferred to an autosampler vial and mixed with 0.5 ml 1 M sodium methoxide solution in methanol for 30 min at 40°C to obtain methyl esters of each fatty acid. Next 0.8 ml of distilled water was added to each vial and after 3 to 5 min 0.5 ml hexane was added. The methyl esters dissolved in the hexane layer and this layer was then transferred to a new vial. The samples were analyzed in a gas chromatograph fitted with flame detectors and capillary columns that were 0.25 mm in diameter and had a film thickness of 0.25 µ. The column temperature was 200°C. Contents of fatty acids in the groat-oil were computed by integrating the peak areas corrected for number of C-H bonds (Craske and Bannon, 1987) and were expressed in g kg^{-1} groat-oil.

For each groat-oil sample the ratio of polyunsaturated plus monounsaturated fatty acids to saturated fatty acids (PMS) was computed as (18:1 + 18:2 + 18:3)/(16:0 + 18:0).

Statistical Analyses

The fatty acids and PMS values for the random lines were subjected to analyses of variance. Locations and genotypes were considered random effects and cycles of selection fixed. Satterthwaite's approximate F-test procedure was used to test for cycle main effects and Fisher's protected L.S.D.-test to compare cycle means and cycle means with parent and check means. For each cycle of selection, the variance component due to genotypes (σ^2_G) was estimated as a linear function of the appropriate mean squares, and it was tested for significance via an F-test. Broad-sense heritability (H^2) was computed on an entry mean basis for each cycle of selection. Exact 90% confidence intervals for H^2 were calculated by applying the method of Knapp et al. (1985).

Orthogonal polynomial regressions of the fatty acids and PMS values on cycles of selection were computed to partition the variation due to cycles into variation due to linear effects, quadratic effects, and deviations from regression. Significance of the linear (β_1) and quadratic (β_q) regression coefficients was determined by testing the mean square of the linear and quadratic effects against the location-cycle interaction mean square. If only the linear regression was significant, response per cycle of selection was $\hat{\beta}_1$. If the quadratic regression also was significant, response per cycle was calculated as $(C_6-C_0)/6$.

Phenotypic correlations (r_{ph}) were computed for each pair of traits within each cycle of selection. The r_{ph}'s were pooled over cycles of selection for each trait pair, and 95% confidence intervals were computed as described by Steel and Torrie (1980). A X^2-test was performed to test for homogeneity of the r_{ph}'s for each pair of traits. If the test was significant, the r_{ph}'s were further examined to determine whether the r_{ph}'s showed trends of change over selection cycles.

RESULTS AND DISCUSSION

The fatty acid composition of groat-oil changed significantly over cycles of selection (Table 1, Fig. 1). Changes in the saturated fatty acids were minor. Palmitate decreased from 172.8 g kg^{-1} in C_0 to 159.4 g kg^{-1} in C_6, and 18:0 increased from 27.6 g kg^{-1} in the C_0 to 31.1 g kg^{-1} in the C_6. The responses were -2.1 g kg^{-1} $cycle^{-1}$ for 16:0 and 0.6 g kg^{-1} $cycle^{-1}$ for 18:0 (Table 2). Palmitate values varied from 131.4 to 212.5 g kg^{-1} and 18:0 values from 15.3 to 47.4 g kg^{-1} (Table 1). No cycle mean for 16:0 was significantly different from that of the checks. Stearate, however, was significantly higher than the means of the parents and checks in each cycle.

Oleate increased from 437.0 g kg^{-1} in the C_0 to 481.3 g kg^{-1} in the C_6 whereas 18:2 and 18:3 decreased from 353.4 to 321.3 g kg^{-1} and from 9.2 to 6.8 g kg^{-1}, respectively (Table 1). Responses for 18:1, 18:2, and 18:3 were 7.4, -5.3, and -0.4 g kg^{-1} $cycle^{-1}$, respectively (Table 2). In every cycle of selection the mean of 18:1 was higher than the means of the parents or checks. The oil of several oat lines contained more than 500 g kg^{-1} 18:1. In each cycle the means of 18:2 and 18:3 were smaller than the means of the parents and checks. The lowest value for 18:3 was 2.3 g kg^{-1} and the highest value for 18:2 was 395.1 g kg^{-1} (Table 1).

PMS values increased significantly over cycles of

Figure 1. Responses of GO, fatty acids, and PMS to six cycles of recurrent selection for GO

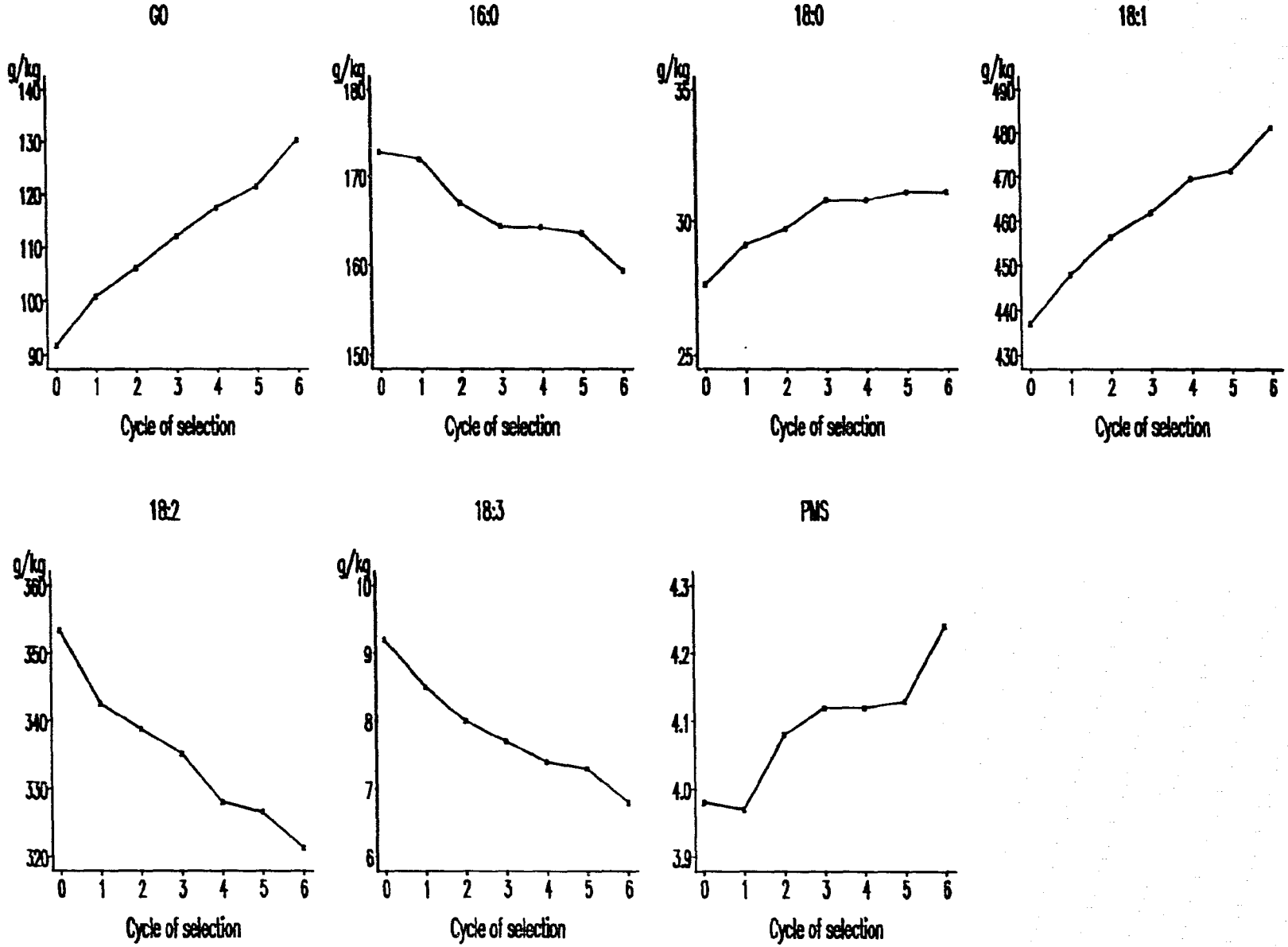
GO
g/kg
140
130
120
110
100
90
0 1 2 3 4 5 6
Cycle of selection
16:0
g/kg
180
170
160
150
0 1 2 3 4 5 6
Cycle of selection
18:0
g/kg
35
30
25
0 1 2 3 4 5 6
Cycle of selection
18:1
g/kg
490
480
470
460
450
440
430
0 1 2 3 4 5 6
Cycle of selection
18:2
g/kg
360
350
340
330
320
0 1 2 3 4 5 6
Cycle of selection
18:3
g/kg
10
9
8
7
6
0 1 2 3 4 5 6
Cycle of selection
PMS
4.3
4.2
4.1
4.0
3.9
0 1 2 3 4 5 6
Cycle of selection

Table 1. Means for fatty acids and PMS values for each cycle of selection and for parents and checks

Cycle	Trait					
	16:0	18:0	18:1	18:2	18:3	PMS
	g kg^{-1}					
Regime 1						
0	172.8	27.6	437.0	353.4	9.2	3.98
1	172.0	29.1	447.9	342.6	8.5	3.97
2	167.0	29.7	456.5	338.8	8.0	4.08
3	164.4	30.8	461.9	335.2	7.7	4.12
4	164.3	30.8	469.6	328.0	7.4	4.12
5	163.6	31.1	471.4	326.6	7.3	4.13
6	159.4	31.1	481.3	321.3	6.8	4.24
$FLSD_{0.05}$	4.9	2.3	5.7	6.0	0.4	0.17
Minimum	131.4	15.3	383.3	292.3	2.3	2.93
Maximum	212.5	47.4	517.1	395.1	12.9	5.41
Parents						
	173.6	25.2	411.7	378.9	10.6	4.02
$FLSD_{0.05}$[a]	4.9	1.9	5.7	5.4	0.4	0.14
Checks						
	166.4	19.6	401.0	400.8	12.2	4.37
$PLSD_{0.05}$[b]	8.7	3.4	9.9	9.5	0.7	0.25

[a]Applicable for comparison of parents with cycle means.

[b]Applicable for comparison of checks with cycle means.

selection. The response was 0.04 $cycle^{-1}$, which shows that the proportion of unsaturated fatty acids in the oat oil increased. PMS values in C_0, C_1, and C_2 were significantly lower than that of the checks. Thus, when compared to the checks, the initial gene pool was low for PMS.

Table 2. Polynomial regressions and responses per cycle of selection for fatty acids and PMS values

Trait	Mean	$\hat{\beta}_1$	$\hat{\beta}_q$	Response cycle^{-1}
16:0, g kg^{-1}	165.7	-2.1**	0.1	-2.1
18:0, g kg^{-1}	30.6	0.6**	-0.1*	0.6
18:1, g kg^{-1}	462.4	6.9**	-0.4*	7.4
18:2, g kg^{-1}	333.6	-5.0**	0.4*	-5.3
18:3, g kg^{-1}	7.7	-0.4**	0.0**	-0.4
PMS	4.13	0.04**	0.00	0.04

*,**Significant at the 0.05 and 0.01 probability levels, respectively.

Average fatty acid profiles of HO-lines, checks, and three other vegetable oils are presented in Table 3. The groat-oil in 20 HO-lines (with a mean GO of 152.2 g kg^{-1}) had considerably lower levels of 18:3 than soybean oil. The high proportion of 18:3 in soybean oil causes flavor, stability, and odor problems (Wilson et al., 1981). The fatty acid profile of HO-lines is characterized by a relatively high level of 18:1 and is, in that respect, comparable to canola (Brassica spp.) oil. Because of the higher levels of saturated fatty acids, PMS values of oil in HO-lines were lower than that of soybean, maize, and canola oils. However, groat-oil in HO-lines is the most balanced oil with respect to saturated, monounsaturated, and polyunsaturated fatty acids. Therefore, groat-oil of oat

Table 3. Means for fatty acid contents and PMS values of HO-lines and checks, and for soybean, maize, and canola

Genotypes	Fatty acids										PMS
	Saturated			Monounsaturated				Polyunsaturated			
	16:0	18:0	Tot.	18:1	20:1	22:1	Tot.	18:2	18:3	Tot.	
	g kg^{-1}										
HO-lines	162	34	196	491	-	-	491	305	8	313	4.11
Checks	166	20	186	401	-	-	401	401	12	413	4.37
Maize[a]	130	40	170	290	-	-	290	540	-	540	4.88
Canola[a]	40	20	60	550	20	10	580	260	100	360	15.67
Soybean[a]	110	40	150	250	-	-	250	510	90	600	5.67

[a]Adapted from deMan (1990).

would be a vegetable oil with a high dietary quality.

Except for 18:3 in C_6, all $\hat{\sigma}^2_G$'s for fatty acids and PMS values were highly significant in each cycle of selection (Table 4). Thus, selection for more favorable fatty acid profiles should be possible. There is an indication that the $\hat{\sigma}^2_G$ for 18:2 decreased with selection for GO. The $\hat{\sigma}^2_G$ for 18:3 in C_6 was not significant which may indicate genetic variability for this fatty acid has been exhausted.

Heritability values for fatty acids and PMS values were high in most cycles of selection (Table 5). They ranged from 0.74 to 0.90, 0.86 to 0.95, 0.78 to 0.89, 0.83 to 0.91, 0.14 to 0.90, and 0.71 to 0.93, for 16:0, 18:0, 18:1, 18:2, and 18:3, respectively. The high H^2's for 16:0, 18:1, and 18:2 agree with earlier reported values (Youngs and Püskülcü, 1976; Thro et al., 1985).

The r_{ph}'s between 16:0 and 18:0 and between 18:0 and 18:1 were not significant (Table 6). GO was strongly and positively associated with 18:1 and negatively with 18:2 and 18:3. The r_{ph}'s between GO and 18:1 were homogeneous over cycles of selection whereas that between GO and 18:2 and GO and 18:3 were not, but no consistent trends were evident. The correlations of GO with 18:1, 18:2, and 18:3 agree with associations reported in oat by Karow and Forsberg (1984), Youngs and Püskülcü (1976), de la Roche et al. (1977), Frey and Hammond (1975), and Forsberg et al. (1974), and in maize by Pamin et al. (1986) and Trifunovic et al. (1975). Youngs

Table 4. Genetic variances ($\hat{\sigma}^2_G$) for fatty acids and PMS values of oat lines within cycles of selection

Cycle	Trait					
	16:0	18:0	18:1	18:2	18:3 x 10^2	PMS x 10
0	55**	23**	154**	204**	61**	37**
1	96**	18**	200**	140**	46**	60**
2	122**	25**	135**	163**	62**	114**
3	108**	16**	117**	108**	86**	112**
4	136**	15**	116**	99**	32**	112**
5	146**	18**	151**	108**	68**	112**
6	72**	17**	85**	87**	7	66**

**Mean square for genotypes significant at the 0.01 probability level.

and Püskülcü (1976) and de la Roche et al. (1977) reported high negative correlations between GO and 16:0 in oat.

The r_{ph} of GO with PMS was small (Table 6). Thus the saturated-unsaturated fatty acid balance in the oil is only moderately dependent on GO. Changes in the fatty acid composition occurred primarily within the saturated and unsaturated classes.

The r_{ph}'s between 16:0 and 18:1, 16:0 and 18:2, 18:0 and 18:2, 18:1 and 18:2, and 18:1 and 18:3 were all highly negative. This indicates a negative association between saturated and unsaturated fatty acids and between monounsaturated and polyunsaturated fatty acids. In most vegetable oils 18:0 is synthesized by elongation of 16:0 and it is the precursor of 18:1 which in turn is the precursor of

Table 5. Broad-sense heritabilities (H^2) for fatty acids and PMS values in groat-oil of oat lines within cycles of selection

Cycle	Trait					
	16:0	18:0	18:1	18:2	18:3	PMS
0	0.74	0.92	0.78	0.85	0.55	0.71
1	0.78	0.89	0.85	0.85	0.70	0.76
2	0.90	0.95	0.86	0.91	0.84	0.93
3	0.86	0.90	0.82	0.84	0.90	0.87
4	0.86	0.86	0.83	0.83	0.67	0.87
5	0.88	0.94	0.89	0.87	0.76	0.88
6	0.78	0.94	0.81	0.86	0.14	0.80
Lower limit[a]	0.58	0.58	0.65	0.73	-0.38	0.53
Upper limit[a]	0.94	0.97	0.93	0.95	0.94	0.96

[a]The smallest lower limit and highest upper limit of all confidence intervals.

18:2 and 18:3 (Lehninger, 1982). Thus the correlations confirm the functional dependence between the fatty acids. The X^2-test was significant for the r_{ph}'s between 16:0 and 18:1 and between 18:1 and 18:2, but there were no trends over cycles of selection.

In summary, recurrent selection for increased GO significantly changed the fatty acid composition in groat-oil of oat. The changes occurred primarily within the saturated and unsaturated classes of fatty acids. Within the saturated class the content of 18:0 increased and within the unsaturated class the content of 18:1 increased and that of 18:2 decreased. The ratio of unsaturated to saturated fatty

Table 6. Phenotypic correlations (r_{ph}) for pairs of traits with confidence intervals and tests of homogeneity

Trait	Trait		
	16:0	18:0	18:1
GO	-0.18 (0.333)[a] (-0.29, -0.08)[b]	0.15 (0.030) (0.05, 0.26)	0.44 (0.312) (0.35, 0.52)
16:0		0.02 (0.099) (-0.09, 0.13)	-0.57 (0.032) (-0.64, -0.49)
18:0			0.00 (0.050) (-0.11, 0.11)
18:1			
18:2			
18:3			

[a] p value of the X^2-test.

[b] 95% confidence interval.

18:2	18:3	PMS
-0.32 (0.008) (-0.41, -0.22)	-0.28 (0.002) (-0.38, -0.18)	0.12 (0.169) (0.01, 0.22)
-0.38 (0.081) (-0.47, -0.28)	0.25 (0.938) (0.14, 0.35)	-0.93 (0.023) (-0.94, -0.91)
-0.41 (0.328) (-0.50, -0.32)	-0.17 (0.009) (-0.27, -0.06)	-0.40 (0.317) (-0.49, -0.31)
-0.51 (0.000) (-0.59, -0.42)	-0.34 (0.176) (-0.43, -0.24)	0.52 (0.070) (0.43, 0.59)
	0.11 (0.190) (0.01, 0.22)	0.49 (0.326) (0.41, 0.57)
		-0.17 (0.771) (-0.27, -0.06)

acids in groat-oil increased over cycles of selection. HO-lines were characterized by high levels of 18:1 in groat-oil.

REFERENCES

Anonymous. 1990. Economic implications of modified soybean traits. Iowa Agric. Home Econ. Exp. Stn. Special report no. 92. Iowa State Univ. Ames, IA.

Bonanome, A., and S.M. Grundy. 1988. Effect of dietary stearic acid on plasma cholesterol and lipoprotein levels. N. Engl. J. Med. 318:1244-1248.

Branson, C.V., and K.J. Frey. 1989. Recurrent selection for groat-oil content in oat. Crop Sci. 29:1382-1387.

Burton, J.W., R.F. Wilson, and C.A. Brim. 1983. Recurrent selection in soybeans. IV. Selection for increased oleic acid percentage in seed oil. Crop Sci. 23:744-747.

Conway, T.F., and F.R. Earle. 1963. Nuclear magnetic resonance for determining oil content of seeds. J. Am. Oil Chem. Soc. 40:265-268.

Craske, J.D., and C.D. Bannon. 1987. Gas liquid chromatography analysis of the fatty acid composition of fats and oils: A total system for high accuracy. J. Am. Oil Chem. Soc. 64:1413-1417.

de la Roche, I.A., V.D. Burrows, and R.I.H. McKenzie. 1977. Variation in lipid composition among strains of oats. Crop Sci. 17:145-148.

deMan, J.M. 1990. Principles of food chemistry. 2nd ed. Van Nostrand Reinhold, New York, NY.

Forsberg, R.A., V.L. Youngs, and H.L. Shands. 1974. Correlations among chemical and agronomic characteristics in certain oat cultivars and selections. Crop Sci. 14:221-224.

Frey, K.J., and E.G. Hammond. 1975. Genetics, characteristics, and utilization of oil in caryopses of oat species. J. Am. Oil Chem. Soc. 52:358-362.

Grundy, S.M. 1987. Monounsaturated fatty acids, plasma cholesterol, and coronary heart disease. Am. J. Clin. Nutr. 45:1168-1175.

Guthrie, H.A. 1989. Introductory nutrition. 7th ed. Times Mirror/Mosby College Publishing, St. Louis, MO.

Hegsted, D.M., R.B. McGandy, M.L. Myers, and F.J. Stare. 1965. Quantitative effects of dietary fat on serum cholesterol in man. Am. J. Clin. Nutr. 17:281-295.

Karow, R.S., and R.A. Forsberg. 1984. Oil composition in parental, F1, and F2 populations of two oat crosses. Crop Sci. 24:629-632.

Knapp, S.J., W.W. Stroup, and W.M. Ross. 1985. Exact confidence intervals for heritability on a progeny mean basis. Crop Sci. 25:192-194.

Lehninger, A.L. 1982. Principles of biochemistry. Worth Publishers, New York, NY.

Misevic, D., and D.E. Alexander. 1989. Twenty-four cycles of phenotypic recurrent selection for percent oil in maize. I. Per se and test-cross performance. Crop Sci. 29:320-324.

Pamin, K., W.A. Compton, C.E. Walker, and D.E. Alexander. 1986. Genetic variation and selection response for oil composition in corn. Crop Sci. 26:279-282.

Schipper, H. 1991. Section II. Three recurrent selection regimes to increase groat-oil content of oat. In H. Schipper. Comparison of three recurrent selection regimes for increasing groat-oil content of oat. Ph.D. dissertation. Iowa State Univ., Ames, IA.

Steel, R.G.D., and J.H. Torrie. 1980. Principles and procedures of statistics. 2nd ed. McGraw-Hill, New York, NY.

Thro, A.M., K.J. Frey, and E.G. Hammond. 1985. Inheritance of palmitic, oleic, linoleic, and linolenic fatty acids in groat-oil of oats. Crop Sci. 25:40-44.

Trifunovic, V. S. Ratkovic, M. Misovic, S. Kapor, and J. Dumanovic. 1975. Variability in content and fatty acid composition of maize oil. Maydica 20:175-183.

Vles, R.O., and J.J. Gottenbos. 1989. Nutritional characteristics and food uses of vegetable oils. p. 63-86. In G. Röbbelen et al. (ed.) Oil crops of the world. McGraw-Hill, New York, NY.

Wilson, R.F., J.W. Burton, and C.A. Brim. 1981. Progress in the selection for altered fatty acid composition in soybeans. Crop Sci. 21:788-791.

Youngs, V.L., and H. Püskülcü. 1976. Variation in fatty acid composition of oat groats from different cultivars. Crop Sci. 16:881-883.

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GENERAL SUMMARY

The efficacy of three recurrent selection regimes for increasing groat-oil content of oat (Avena sativa L.) was investigated. One cycle of recurrent selection for regime 1 consisted of selection among S_0 plants in the field and intermating selected $S_{0:1}$ lines in the greenhouse. One year was needed to complete a cycle of this regime. Regime 2 was similar to regime 1 except that the evaluation of S_0 plants was done in the greenhouse. Three generations of oat can be grown in the greenhouse each year so 1.5 cycles could be conducted annually. In regime 3 selection was carried out in two phases. First, selection was made among S_0 plants grown in the field, and second, selection occurred among and within greenhouse-grown $S_{0:1}$ progenies from selected S_0 plants. Selected $S_{1:2}$ lines were intermated in the greenhouse. Regime 3 required three generations per cycle, one in the field and two in the greenhouse, and one cycle was completed per year.

To investigate whether greenhouse selection for higher groat-oil content is effective, 48 oat lines were evaluated for groat-oil content in a replicated experiment in the field and greenhouse. A model suggested by Falconer (1952) was used to determine whether groat-oil contents in the field and in the greenhouse were determined by the same set of genes. The predicted genetic gains in groat-oil content for the

three recurrent selection regimes were computed utilizing the genetic gain equation of Eberhart (1970). Gain in groat-oil content from selection in the greenhouse would be 68% as effective as from selection in the field. And when using 300 plants per cycle and a 10% selection intensity, predicted annual gains were 9.45, 4.57, and 11.58 g kg^{-1} for regimes 1, 2, and 3, respectively. Thus, based on predicted gains, regime 2 was not efficient and regime 3 was the most effective for elevating groat-oil content in oat.

Six cycles of recurrent selection for regime 1, two cycles of regime 2, and 2.5 cycles of regime 3 were evaluated in a replicated field experiment grown at two locations. Actual annual gains in groat-oil content were 6.04, 5.85, and 11.98 g kg^{-1} for regimes 1, 2, and 3, respectively. Annual gains for regimes 1 and 2 were not significantly different. In regime 3, selection in the field and in the greenhouse both contributed to the increase in groat-oil content. In all cycles of selection genetic variances for groat-oil content were significant and heritabilites were high. Five of the ten lines with the highest oil yield in this study, had grain yields that were significantly higher than the mean of the check cultivars.

Line M022-4-5 had the highest average groat-oil content at 162.85 g kg^{-1}. Frey and Hammond (1975) calculated that a groat-oil content of 160 g kg^{-1} is needed for economical extraction of oil from oat. Because the results indicate

that continued increases in groat-oil content can be expected, oat lines with even higher oil content will occur.

Selection for groat-oil content resulted in significant correlated increases in oil yield in regimes 1 and 3. In the same regimes, however, significant decreases occurred for grain yield, seed weight, and test weight. Heading date decreased in regime 1 but increased in regime 3. Further, groat fraction and plant height decreased in regimes 1 and 3, respectively. Significant changes did not occur for harvest index. Factor analysis indicated that groat-oil content and grain yield can be increased simultaneously, and that continued selection for groat-oil content will cause reductions in seed weight, test weight, and groat fraction.

The results of the factor analyses led to the proposal of a new recurrent selection regime. A cycle of this regime begins with selection for groat-oil content among field-grown S_0 plants. Then, seed from selected plants is increased in the greenhouse during the winter. $S_{0:2}$ lines are evaluated the following summer in a replicated field experiment at two or more locations. A restricted selection index is used to maximize the genetic gain in groat-oil content while holding agronomic traits to no change. Finally, selected $S_{2:3}$ lines are intermated during the following winter season. One cycle of recurrent selection with this regime requires two years to complete, but because only two generations per year are needed, it will be applicable in more breeding programs.

To study the effect of increasing the groat-oil content on the fatty acid composition, fatty acid contents were determined for 50 oat lines from each cycle of selection of regime 1. The PMS ratio increased significantly over cycles. Correlated changes in the fatty acid composition occurred primarily within the saturated and unsaturated classes of fatty acids. A major increase occurred in oleate content and a similar decrease occurred in linoleate content. The average fatty acid profile of 20 oat lines with a mean groat-oil content of 152.2 g kg^{-1}, was characterized by a high level of monounsaturated fatty acids.

ADDITIONAL REFERENCES

Alexander, D.E. 1988. Breeding special nutritional and industrial types. p. 869-880. In G.F. Sprague and J.W. Dudley (ed.) Corn and corn improvement. ASA, CSSA, and SSSA, Madison, WI.

Appelqvist, L.A. 1989. The chemical nature of vegetable oils. p. 22-37. In G. Röbbelen et al. (ed.) Oil crops of the world. McGraw-Hill, New York, NY.

Avey, D.P., H.W. Ohm, F.L. Patterson, and W.E. Nyquist. 1982. Three cycles of simple recurrent selection for early heading in winter wheat. Crop Sci. 22:908-912.

Baker, R.J., and R.I.H. McKenzie. 1972. Heritability of oil content in oats, Avena sativa L. Crop Sci. 12:201-202.

Bhatia, C.R., and R. Rabson. 1976. Bioenergetic considerations in cereal breeding for protein improvement. Science 194:1418-1420.

Bonanome, A, and S.M. Grundy. 1988. Effect of dietary stearic acid on plasma cholesterol and lipoprotein levels. N. Engl. J. Med. 318:1244-1248.

Branson, C.V., and K.J. Frey. 1989a. Recurrent selection for groat oil content in oat. Crop Sci. 29:1382-1387.

Branson, C.V., and K.J. Frey. 1989b. Correlated response to recurrent selection for groat-oil content in oats. Euphytica 43:21-28.

Bregitzer, P.P., D.D. Stuthman, R.L. McGraw, and T.S. Payne. 1987. Morphological changes associated with three cycles of recurrent selection for grain yield improvement in oat. Crop Sci. 27:165-168.

Brim, C.A., and C.W. Stuber. 1973. Application of genetic male sterility to recurrent selection schemes in soybean. Crop Sci. 13:528-530.

Brown, C.M., and A.N. Aryeetey. 1973. Maternal control of oil content in oats (Avena sativa L.). Crop Sci. 13:120-121.

Brown, C.M., D.E. Alexander, and S.G. Carmer. 1966. Variation in oil content and its relation to other characteristics in oats (Avena sativa L.). Crop Sci. 6:190-191.

Brown, C.M., A.N. Aryeetey, and S.N. Dubey. 1974. Inheritance and combining ability for oil content in oats (Avena sativa L.). Crop Sci. 14:67-69.

Burton, J.W., and C.A. Brim. 1981. Recurrent selection in soybeans. III. Selection for increased percent oil in seeds. Crop Scl. 21:31-34.

Busch, R.H., and K. Kofoid. 1982. Recurrent selection for kernel weight in spring wheat. Crop Sci. 22:568-572.

Byrne, I., and D.C. Rasmusson. 1974. Recurrent selection for mineral content in wheat and barley. Euphytica 23: 241-249.

Crosbie, T.M., R.B. Pearce, and J.J. Mock. 1981. Recurrent phenotypic selection for high and low photosynthesis in two maize populations. Crop Sci. 21:736-740.

de la Roche, I.A., V.D. Burrows, and R.I.H. McKenzie. 1977. Variation in lipid composition among strains of oats. Crop Sci. 17:145-148.

deMan, J.M. 1990. Principles of food chemistry. 2nd ed. Van Nostrand Reinhold, New York, NY.

Eberhart, S.A. 1970. Factors effecting efficiencies of breeding methods. African Soils 15:669-680.

Elliot, A.C., A.M. Thro, and K.J. Frey. 1985. Inheritance of groat-oil content and several other traits in inter- and intra-specific oat matings. Iowa State J. Res. 60:13-24.

Falconer, D.S. 1952. The problem of environment and selection. Am. Nat. 86:293-298.

Falconer, D.S. 1981. Introduction to quantitative genetics. 2nd ed. Longman, London, England.

Fehr, W.R. 1987. Soybean. p. 533-576. In W.R. Fehr (ed.) Principles of cultivar development. II. Crop species. MacMillan, New York, NY.

Foroughi-Weber, B., and G. Wenzel. 1990. Recurrent selection alternating with haploid steps - a rapid breeding procedure for combining agronomic traits in inbreeders. Theor. Appl. Genet. 80:564-568.

Forsberg, R.A., and H.L. Shands. 1989. Oat breeding. p. 167-207. In J. Janick (ed.) Plant breeding reviews. Vol. 6. AVI publishing, Westport, CT.

Forsberg, R.A., V.L. Youngs, and H.L. Shands. 1974. Correlations among chemical and agronomic characteristics in certain oat cultivars and selections. Crop Sci. 14:221-224.

Frey, K.J., and E.G. Hammond. 1975. Genetics, characteristics, and utilization of oil in caryopses of oat species. J. Am. Oil Chem. Soc. 52:358-362.

Frey, K.J., E.G. Hammond, and P.K. Lawrence. 1975. Inheritance of oil percentage in interspecific crosses of hexaploid oats. Crop Sci. 15:94-95.

Frey, K.J., J.K. McFerson, and C.V. Branson. 1988. A procedure for one cycle of recurrent selection per year with spring-sown small grains. Crop Sci. 28:855-856.

Gilmore, E.C. 1964. Suggested method of using reciprocal recurrent selection in some naturally self-pollinated species. Crop Sci. 4:323-325.

Grundy, S.M. 1987. Monounsaturated fatty acids, plasma cholesterol, and coronary heart disease. Am. J. Clin. Nutr. 45:1168-1175.

Gullord, M. 1980. Oil and protein content and its relation to other characteristics in oats (Avena spp.). Acta Agric. Scand. 30:216-218.

Gullord, M. 1986. Oil and protein content in oats (Avena sativa L.). p. 210-213. In D.A. Lawes and H. Thomas (ed.) Proc. 2nd Int. Oats Conf. Aberystwyth, Wales. 15-18 July 1985. Martinus Nijhoff Publishers, Dordrecht, The Netherlands.

Guthrie, H.A. 1989. Introductory nutrition. 7th ed. Times Mirror/Mosby College Publishing, St. Louis, MO.

Hallauer, A.R. 1981. Selection and breeding methods. p. 3-55. In K.J. Frey (ed.) Plant Breeding II. Iowa State Univ. Press, Ames, IA.

Hallauer, A.R. 1985. Compendium of recurrent selection methods and their application. CRC Crit. Rev. Plant Sci. 3:1-33.

Hallauer, A.R. and J.B. Miranda, Fo. 1988. Quantitative genetics in maize breeding. 2nd ed. Iowa State Univ. Press, Ames, IA.

Hammond, E.G. 1983. Oat lipids. p. 331-352. In P.J. Barnes (ed.) Lipids in cereal technology. Acad. Press, New York, NY.

Hegsted, D.M., R.B. McGandy, M.L. Myers, and F.J. Stare. 1965. Quantitative effects of dietary fat on serum cholesterol in man. Am. J. Clin. Nutr. 17:281-295.

Hutchinson, J.B., and H.F. Martin. 1952. The measurement of lipase activity in oat products. J. Sci. Food Agric. 3:312-315.

Hutchinson, J.B., and H.F. Martin. 1955. The chemical composition of oats. I. The oil and free fatty acid content of oats and groats. J. Agric. Sci. Camb. 45:411-418.

Jensen, N.F. 1970. A diallel selective mating system for cereal breeding. Crop Sci. 10:629-635.

Jensen, N.F. 1988. Plant breeding methodology. John Wiley & Sons, New York, NY.

Kalbasi-Ashtari, A., and E.G. Hammond. 1977. Oat oil: refining and stability. J. Am. Oil Chem. Soc. 54: 305-307.

Karow, R.S., and R.A. Forsberg. 1984. Oil composition in parental, F1, and F2 populations of two oat crosses. Crop Sci. 24:629-632.

Klein, S.J. 1990. Recurrent selection for test weight in oat. MS thesis. Iowa State Univ., Ames, IA.

Lehninger, A.L. 1982. Principles of biochemistry. Worth Publishers, New York, NY.

Löffler, C.M., R.H. Busch, and J.V. Wiersma. 1983. Recurrent selection for grain protein percentage in hard red spring wheat. Crop Sci. 23:1097-1101.

McDaniel, M.E., H.B. Kim, and B.R. Hathcock. 1967. Approach crossing of oats (Avena spp.). Crop Sci. 7:538-540.

McPerson, J.K., and K.J. Frey. 1990. Three selection strategies to increase protein yield in oats. J. Genet. Breed. 44:39-48.

McNeal, F.H., C.F. McGuire, and M.A. Berg. 1978. Recurrent selection for grain protein content in spring wheat. Crop Sci. 18:779-782.

Miller, R.I., J.W. Dudley, and D.E. Alexander. 1981. High intensity selection for percent oil in corn. Crop Sci. 21:432-437.

Misevic, D., and D.E. Alexander. 1989. Twenty-four cycles of phenotypic recurrent selection for percent oil in maize. I. Per se and test-cross performance. Crop Sci. 29:320-324.

Mitra, R., and C.R. Bhatia. 1979. Bioenergetic considerations in the improvement of oil content and quality in oil-seed crops. Theor. Appl. Genet. 54: 41-47.

Parlevliet, J.E., and A. van Ommeren. 1988a. Accumulation of partial resistance in barley to barley leaf rust and powdery mildew through recurrent selection against susceptibility. Euphytica 37:261-274.

Parlevliet, J.E., and A. van Ommeren. 1988b. Recurrent selection for grain yield in early generations of two barley populations. Euphytica 38:175-184.

Patel, J.D., E. Reinbergs, and S.O. Fejer. 1985. Recurrent selection in double-haploid populations of barley (Hordeum vulgare L.). Can J. Genet. Cytol. 27:172-177.

Payne, T.S., D.D. Stuthman, L.R. McGraw, and P.P. Bregitzer. 1986. Physiological changes associated with three cycles of recurrent selection for grain yield improved in oats. Crop Sci. 26:734-736.

Penning de Vries, F.W.T., A.H.M. Brunsting, and H.H. van Laar. 1974. Products, requirements, and efficiency of biosynthesis: a quantitative approach. J. Theor. Biol. 45:339-377.

Peterson, D.M. 1976. Protein concentration, concentration of protein fractions, and amino acid balance in oats. Crop Sci. 16:663-666.

Price, P.B., and J.G. Parsons. 1975. Lipids of seven cereal grains. J. Am. Oil Chem. Soc. 52:490-493.

Rezai, A., and K.J. Frey. 1988. Variation in relation to geographical distribution of wild oats - seed traits. Euphytica 39:113-118.

Sorrels, M.E., and S.E. Fritz. 1982. Application of a dominant male-sterile allele to the improvement of self-pollinated crops. Crop Sci. 22:1033-1035.

Stuke, H. 1961. Untersuchungen über den Einfluß von Umweltfaktoren auf den Rohfettgehalt des Hafers. Z. Pflanzenzüchtung 45:143-177.

Thro, A.M., and K.J. Frey. 1984. Relationship between groat-oil content and grain yield of oats (Avena sativa L.). Proc. Iowa Acad. Sci. 91:85-86.

Thro, A.M., and K.J. Frey. 1985. Inheritance of groat-oil content and high-oil selection in oats (Avena sativa L.). Euphytica 34:251-263.

Vles, R.O., and J.J. Gottenbos. 1989. Nutritional characteristics and food uses of vegetable oils. p. 63-86. In G. Röbbelen et al. (ed.) Oil crops of the world. McGraw-Hill. New York, NY.

Weber, E.J. 1973. Structure and function of cereals components as related to their potential industrial utilization. p. 161-206. In Y. Pomeranz (ed.) Industrial uses of cereals. Am. Assoc. Cereal Chem., St. Paul, MN.

Welch, R.W. 1974. The effect of winter and spring sowing on the grain composition of oat variaties. J. Agric. Sci. Camb. 83:275-279.

Welch, R.W. 1975. Fatty acid composition of grain from winter and spring sown oats, barley, and wheat. J. Sci. Food Agric. 26:429-435.

Yarosh, N.P., and G.K. Nizova. 1988. Oil percentage and fatty acid composition of oil in the grain of cultivated and red oats. (In Russian). Res. Bull. N.I. Vavilov Inst. Plant Ind. 180:18-22.

Youngs, V.L. 1972. Protein distribution in the oat kernel. Cereal Chem. 49:407-411.

Youngs, V.L., and R.A. Forsberg. 1979. Protein-oil relationships in oats. Crop Sci. 19:798-802.

Youngs, V.L., and R.A. Forsberg. 1987. Oat. p. 457-499. In R.A. Olson and K.J. Frey (ed.) Nutritional quality of cereal grains: genetic and agronomic improvement. ASA, CSSA, and SSSA, Madison, WI.

Youngs, V.L., and H. Püskülcü. 1976. Variation in fatty acid composition of oat groats from different cultivars. Crop Sci. 16:881-883.

Youngs, V.L., M. Püskülcü, and R.R. Smith. 1977. Oat lipids. I. Composition and distribution of lipid components in two oat cultivars. Cereal Chem. 54: 803-812.

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